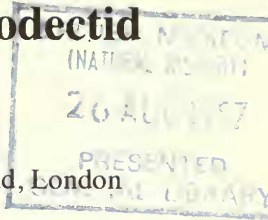


A cladistic analysis and classification of trichodectid mammal lice (Phthiraptera: Ischnocera)

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Synopsis

Observations on phthirapteran morphology are analysed with particular reference to the Trichodectidae. Problems of structure, homology and nomenclature associated with major morphological features are briefly reviewed and solutions suggested where possible; where appropriate, the morphological terminology is clarified. A cladistic analysis of the 351 species and subspecies of Trichodectidae is carried out using the states of 187 characters, and the taxa are re-classified in accordance with the results and the principles of phyletic sequencing. Twenty genera are accepted in five subfamilies. Ten of the genera are divided into 27 subgenera. This necessitates the description of one new subfamily, three new genera and four new subgenera. Three genera are newly synonymised, eight genera and subgenera are recalled from synonymy, and four genera are reduced to subgenera. The generic placements of 106 species and subspecies are changed. Keys to the subfamilies, genera and subgenera are provided, and the genera and subgenera are described.

Introduction

The Trichodectidae is a family of ischnoceran chewing lice parasitic on mammals. There are 351 described species and subspecies grouped into between 13 and 39 genera, various workers having widely differing views on generic limits. The classification of the Trichodectidae at the generic level is perhaps more confused than that of any other group of lice (Hopkins, 1949, 1960; Emerson & Price, 1981) and no workable keys to genera are available. The confusion and

disagreement surrounding the classification of the family persists despite a sound basis of taxonomic knowledge at the species level, derived largely from the works of Werneck (1948, 1950), although this author did not attempt to produce any keys.

The purpose of this study is to present a classification of the species of Trichodectidae and to describe and provide a key to the recognised genera and subgenera. The foundation of the classification proposed below is a cladistic analysis, and for the purpose of determining character polarity in that analysis a suitable out-group had to be identified first. Ideally this out-group should be the sister-group of the taxon studied, and in this case would be expected to be a group in the same suborder, the Ischnocera. However, the holophyly of the Ischnocera has not been demonstrated (Lyal, 1985), although there is evidence that indicates the holophyly of a group comprising most of the Ischnocera (including the Trichodectidae). The classification of the Ischnocera is unsettled, and the sister-group of the Trichodectidae has not been identified. A single teneral male specimen of a possible sister-group has been seen, purportedly collected from a corvid in Austria. The specimen has the single tarsal claws of a mammal parasite, but no other apomorphies of the Trichodectidae, although it has the same general facies as members of the family. As out-group, therefore, the Ischnocera s.l. is used, reference being made where appropriate to the other three suborders of Phthiraptera (Lyal, 1985).

The term 'holophyletic' is used below to refer to groups of taxa comprising a single ancestral species (known or inferred) and all of its descendants. The more familiar term 'monophyletic' is avoided because ambiguities in its use have caused misunderstandings in the resolution of systematic problems.

Scale lines equivalent to 50 μm are given in most figures.

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Method of systematic analysis

Systematic analysis is carried out in order to determine 'relationships' between different taxa, the relationships discovered being employed to study some aspect of the biology or evolution of the taxa and/or to provide a framework for their classification. Taxa may be deemed to be 'related' according to a number of different criteria, so the type of analysis performed is dictated by the requirements of other studies to be undertaken. In this case the systematic analysis is preliminary to an examination of the phylogenetic linkages between Trichodectidae and their hosts (Lyal, in prep., a). The relationships required from the analysis are therefore phylogenetic in nature. Although it has been suggested that phylogenetic relationships can be determined by phenetic analysis (Sneath & Sokal, 1973), this is generally believed not to be the case, and a phyletic analysis is required (Wiley, 1981). In this study a manual cladistic analysis was deemed most suitable as computerized methods of sufficient power and capacity were unavailable when the study was initiated (Lyal, 1983).

The first stage in the analysis was a character survey of all species of the family, with the aim of discovering suitable apomorphies. As analysis proceeded some characters initially selected were rejected, if the polarity of their states could not be determined, or if their apomorphic states were restricted to single species.

The observations were recorded in a data matrix, but it rapidly became apparent that this

matrix was too large to be manipulated conveniently. Preliminary inspection of the taxa had led to the recognition of sufficient apomorphies to divide the family into five or six plausible holophyletic groups, so secondary data matrices were compiled for each of these. The smaller number of species and apomorphies then necessary on each of these matrices enabled manual analysis to proceed. These matrices were inclusive rather than exclusive, and taxa with low probabilities of membership were included; as a consequence some taxa were included in more than one matrix. The matrices were examined and taxa or holophyletic groups sharing the greatest number of synapomorphies were united as sister-groups. This process was continued until the cladistic relationships within each matrix were resolved as fully as possible. The full matrix was then compiled using the largest holophyletic groups identified in the analysis of the secondary matrices. This matrix was then analysed using the same technique and the full cladogram drawn. The cladogram, which gave the full distribution of apomorphies, was examined to ensure that the most parsimonious distribution of apomorphies had been achieved.

Character states were weighted by a simple 'gain' or 'loss' criterion. 'Loss' states were only used in the analysis where 'gain' states were not available, and after 'gain' states had been used to resolve the cladogram as fully as possible. It follows that, whereas the distribution of 'gain' states should be maximally parsimonious over the cladogram, this is unlikely to be the case for 'loss' states.

Relationship of systematic analysis and classification

Biological classifications are designed not only to enable the taxa classified to be located in the literature and in collections, but also to store information about those taxa. In many cases the nature of this information is not clear from the classification, and taxa are grouped together on the basis of some ill-defined combination of phenetic and phyletic relationships. The type of information stored in the classification (i.e. the type of relationship used in its construction) may, however, be indicated precisely, and the classification used as an efficient data-retrieval system. This can only be done by utilisation of cladistic information alone; attempts to incorporate phenetic or anagenetic information lower the retrieval facility (Cracraft, 1974).

The method whereby the classification was constructed from the results of the cladistic analysis in this study was by using both rank and sequence in which taxa of equal rank are listed (G. Nelson, 1972, 1974; Cracraft, 1974; Wiley, 1979, 1981). This process has been termed phyletic sequencing (Cracraft, 1974). The convention employed is that within a classification holophyletic taxa of equal rank are listed ('sequenced') so that each taxon is the sister-group of all those taxa of the same rank (and within the same taxon of immediately higher rank) listed below it in the classification (modified from Cracraft, 1974). Use of this criterion allows recovery of a dichotomously-branching cladogram from the classification. However, holophyletic groups with a trichotomous or polychotomous interrelationship must also be accommodated. Wiley (1979) recommends that these be placed in the classification with equal rank and be noted as '*sedis mutabilis*' to indicate that their order is unknown or interchangeable. It must be remembered that this convention is for a formal classification, not for regular use in discussion.

All hierarchical groups may be sequenced, but it is probably more efficient to employ informal groups below the subgenus level, especially with larger genera.

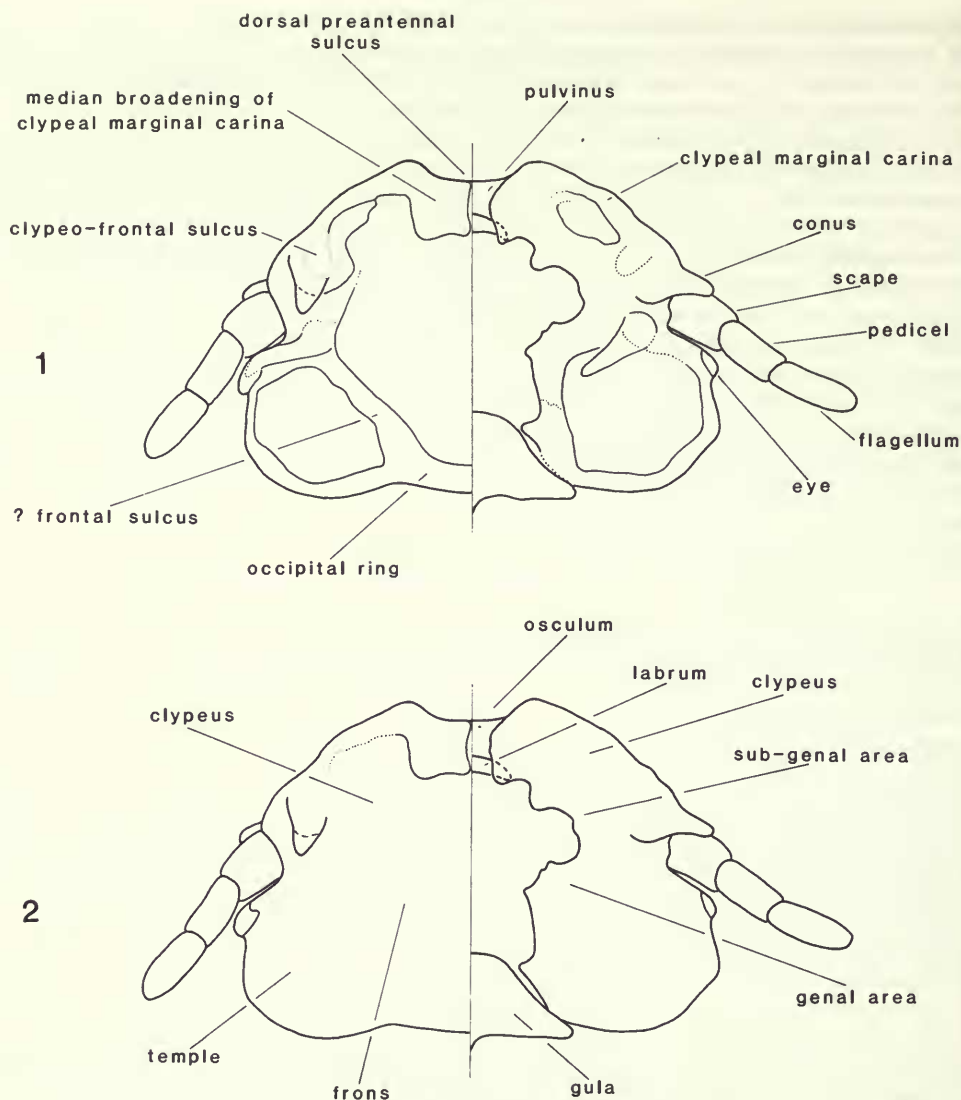
Morphology

The discussion below is intended to clarify morphological terms used in this study, to point out structures of taxonomic or systematic interest, and to describe briefly the morphology of the insects.

Head

Figures 1 and 2 depict the dorsal and ventral aspects of a generalised trichodectid head with the regions and major features labelled with the terms used in this study.

The internal carinae of the head are strongly developed in many species, and differences in the



Figs 1, 2 Terminology applied to trichodectid head, modified slightly from Symmons (1952). Mandible, maxilla, hypopharynx and labium omitted. 1, structures of head (♀); 2, regions of head (♀).

degree of sclerotisation and position are useful taxonomically, particularly at the species level. The postoccipital sulcus is marked by a greatly-developed internal carina ('occipital ring') projecting posteriorly into the thorax; this structure is present in many other lice, but rarely so well developed.

The postero-lateral margins of the head ('temple margins') are more or less rounded and may be produced at the postero-lateral angles in some species. The lengths of the setae on the postero-lateral angles may provide characters of taxonomic value. The eyes are positioned adjacent to the antennae or more posteriorly; in some species (e.g. those in the genus *Cebidicola*) the eyes occupy lateral projections.

Anterior to the antennal socket the margin of the head is produced into a variable sclerotised conus (Fig. 1), but the trabecula (Clay, 1946) is absent. A sclerotised conical projection from the dorsal nodus of the clypeo-frontal sulcus may be present projecting parallel to the margin of the antennal socket. This projection is frequently present in only one sex of a species.

The anterior margin of the head may, in plan, form an unbroken arc ('circumfasciate head'), but in most Trichodectidae it is interrupted medially by the pulvinus or the osculum (Symmons, 1952). The pulvinus is a thick bilobed pad of unsclerotised tissue developed from the clypeolabral suture, and is found in all Ischnocera (Fig. 1). The osculum is a median indentation of the anterior margin of the head (Fig. 2). When the insect is at rest the pulvinus and osculum have been observed to be applied to the hair of the host (see discussion of mandibular morphology below). The width of the osculum is therefore probably influenced by the diameter of the hair in the region of the host's body inhabited by the louse. In cases where the pulvinus fails to reach the anterior margin of the head a small ventral sulcus ('ventral preantennal sulcus' of Clay, 1951) may connect it to the margin or osculum. Many species have a small dorsal preantennal sulcus (Clay, 1951) also interrupting the anterior margin medially.

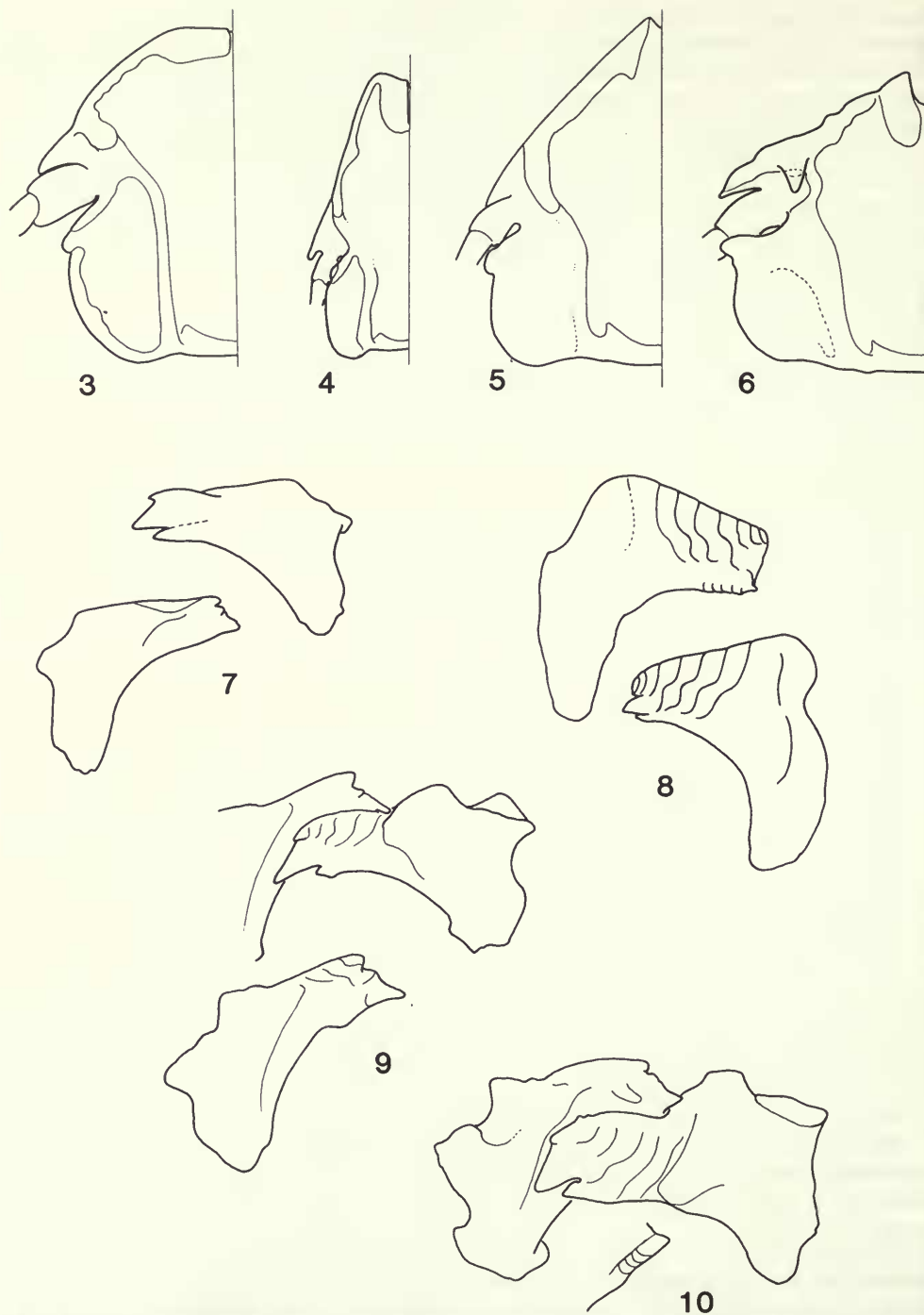
Between the antennae and the osculum the margin of the head may, in plan, be shallowly or broadly convex, sinuate or straight (Figs 3–6); sclerotisation along the margin (forming the 'clypeal marginal carina') may be minimal or heavy, but is usually pronounced in the median dorsal region (Fig. 1). Much of the variation is possibly influenced by the density and texture of the hair of the host.

Only two structures of the mouthparts need be mentioned, the mandibles and the cibarial sclerite.

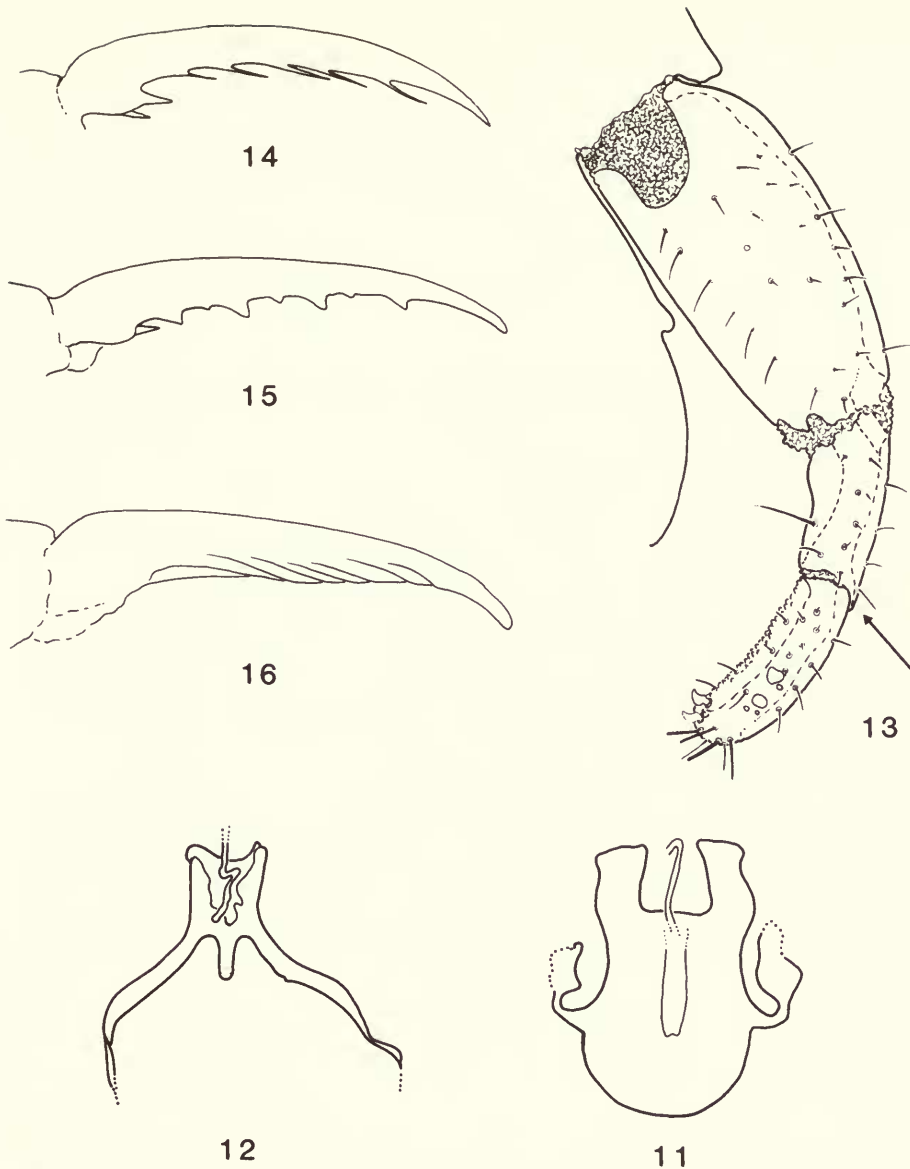
The mandibles of Trichodectidae, like those of many other Amblycera and Ischnocera, are asymmetric. There are three apical teeth on the right mandible and two on the left; on the right the centre tooth is generally longest, whilst on the left the posterior tooth is normally the better developed (Figs 7–10). Mandibular asymmetry is considered by Snodgrass (1935) to be a feature of insects that masticate their food, and the lack of asymmetry in the mandibles of some species of *Ricinus* (Amblycera) is associated by B. Nelson (1972) with blood-feeding in those species. *Trichodectes canis*, the only trichodectid known to take blood meals (Bouvier, 1945), has dimorphic mandibles, as do all other Trichodectidae.

In addition to the collection and preparation of food the mandibles of Trichodectidae are employed in anchoring the insect. When at rest, *Trichodectes canis* and *T. melis* have been observed to enclose a hair in the pulvinus with the mandibles and whilst in this position may completely release the grip of the tarsal claws and straighten the legs laterally from the body. The insect is then held on only by the mandibles. In addition to the species above, specimens of *Felicola* sp. collected from dried museum skins have been found in this position, and specimens of most genera have been found preserved in alcohol clinging to single hairs by their mandibles alone. The selective pressures on the mandibles of Trichodectidae are different, therefore, from those operating on lice that do not have a mandibular anchoring mechanism, and possibly precludes the assumption of monomorphy in blood-feeding species. The 'interior' face of the right or of both mandibles may be ridged, so that when the mandibles are folded closed, the ridges on one mandible are not covered by the other, and all or most of the exposed mandibular area is ridged. The ridges are therefore not positioned in such a way that they can act against one another, and it is suggested that they are developed to prevent the mandibles slipping on a hair when clasp ing it (Figs 8–10). When the mandibles are closed, the right is always interior to the left, which may have a concavity to receive it (Figs 7, 9, 10); the left mandible is not then kept by the right from contact with the hair, and the greatest possible mandibular area is utilised. In some species the right mandible has a basal notch on the anterior margin, which receives the tip of the left mandible (Figs 7, 10); this feature may act in concert with the restraint of the right mandible to 'lock' the mandibles closed about a hair. Although, as said above, none of the Trichodectidae have monomorphic mandibles, the mandibles of *Damalinia* (*T.*) *conectens* (Fig. 7) are very slender and pointed, and the centre tooth of the right mandible of *Dasyonyx* spp. and *Eurytrichodectes* spp. (Fig. 9) is long and pointed, suggesting in each case a piercing function and thus possible haemophagy. In contrast, the mandibles of *Damalinia* (*T.*) *indica* (Fig. 8) are blunt and broad, suggesting an adaptation to grinding and chewing.

The sitophore sclerite (Figs 11, 12) varies considerably in the Psocodea (Cummings, 1913; Haub, 1967, 1972, 1973, 1977). The form of the sclerite, particularly of its posterior border, is obscured in slide-mounted specimens, and differential inclination of the specimens may change



Figs 3-10 Variation in trichodectid head and mouthpart structure. 3-6, ♀ head, dorsal aspect, of (3) *Bovicola caprae*; (4) *Damalinia lineata*; (5) *Felicola subrostratus*; (6) *Trichodectes zorillae*. 7-10, mandibles, dorsal aspect, of (7) *Damalinia conectens*; (8) *Damalinia indica*; (9) *Eurytrichodectes paradoxus*, showing mandibles interlocking; (10) *Trichodectes canis*, with detail of postero-dorsal margin of left mandible.



Figs 11–16 Trichodectid morphology. 11, *Damalinia neotheileri*, sitophore sclerite. 12, *Bovicola hemitragi*, sitophore sclerite. 13, *Damalinia indica*, right antenna of ♂, dorsal, arrow indicating prolongation of antero-ventral pedicel margin. 14–16, lateral aspect of metatarsal claws of (14) *Dasyonyx* (*D.*) *smallwoodae*; (15) *Dasyonyx* (*N.*) *diacanthus*; (16) *Eurytrichodectes paradoxus*.

the apparent dimensions (Haub, 1977). Trichodectidae differ from other Psocodea in having an open posterior border to the sclerite, a character state identified by Haub (1973) as plesiomorphic, but which is almost certainly apomorphic. Within the family the sclerite is present in all species and the form is fairly constant (Fig. 11), although in two species groups the posterior arms are extended laterally (Fig. 12) and the sclerite is difficult to see. The minor variation in the form of the sclerite at the species level is so far unexploited in taxonomic study.

The sitophore sclerite is cup-shaped, and is opposed on the dorsal surface of the sitophore by a closely-fitting projection, the epipharyngeal crest. These two structures have been identified as a 'mortar and pestle' for grinding food (Weber, 1936) and as components of a salivary pump

(Buckup, 1959; Kéler, 1966). Rudolph (1982*a*, 1982*b*, 1983) demonstrates that it is a pump, sucking water absorbed from the atmosphere onto the lingual sclerites through the Y-shaped duct linking these and the sitophore sclerite.

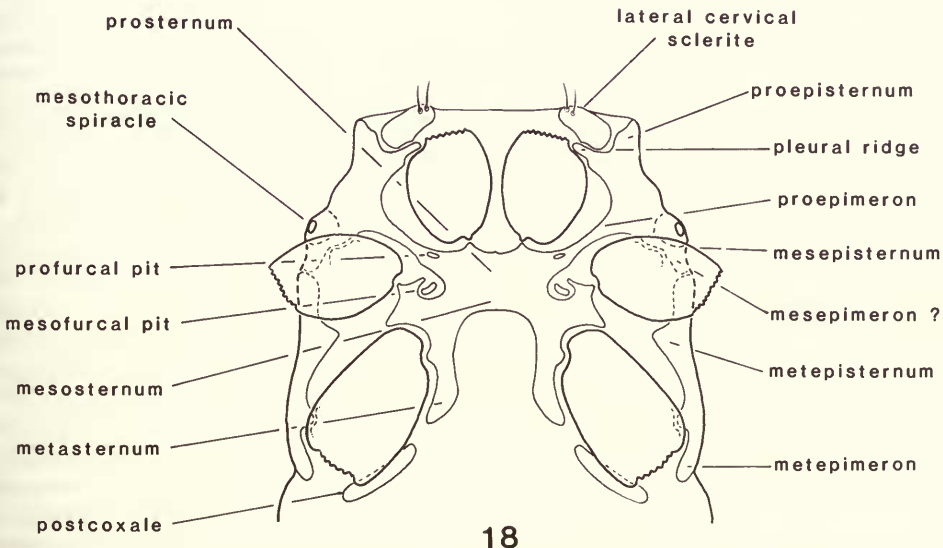
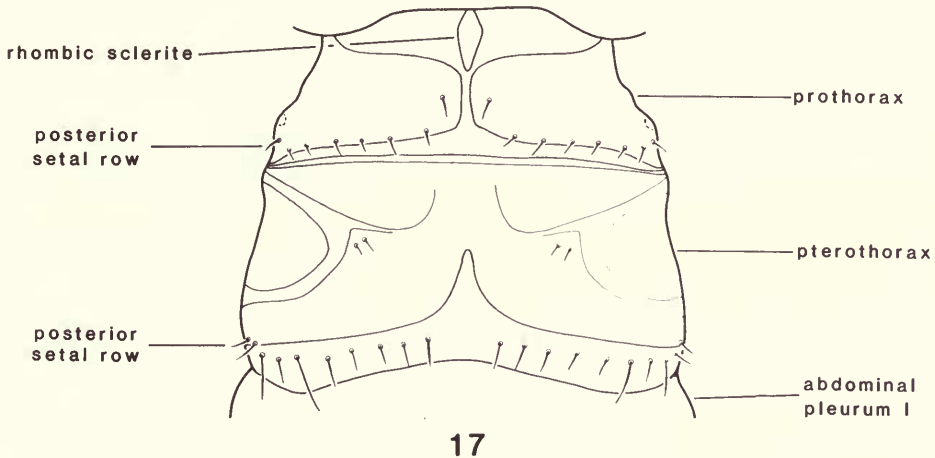
The antennae are made up of a scape, pedicel and flagellum. In common with other Thysanura-Pterygota the pedicel and flagellum are annulations formed by subdivision of a single segment (Imms, 1939; Matsuda, 1965). Consequently, the only intrinsic muscles of the antennae are in the scape and insert on the pedicel, moving the pedicel and flagellum as a unit; the scape itself is moved by muscles inserted on its basal margin and arising on the anterior arms of the tentorium. The positions of the muscle insertions on the scape and pedicel are such that the antenna can be moved through 360 degrees, but there is no muscular mechanism for flexing the flagellum. Whilst the prime function of the antenna is sensory, secondary modification in the male has taken place in some Ischnocera (including almost all Trichodectidae) and some Anoplura, the antennae being used to clasp the female round the abdomen during copulation (Kéler, 1938*a*; Sikora & Eichler, 1941; Lyal, in prep., *b*). This development has led to an increase in length and degree of sclerotisation of the pedicel and flagellomeres and an increase in strength of the antennal muscles. The intrinsic muscles of the scape are enlarged and the scape expanded; the extrinsic muscles are also enlarged and the head concomitantly broader in the male than in the female. To facilitate free movement of the flagellum the joint between the scape and the pedicel is broad and membranous (other than at the two articulatory points). However, because there is no direct muscular control of the flagellum, the degree of free movement relative to the pedicel must be limited, so that control may be effected by the intrinsic muscles of the scape. Observations made in this study reveal that the apex of the pedicel is angled relative to the long axis of the annulation, the longest margin of the pedicel being the antero-ventral (Fig. 13). There is very little membrane between the pedicel and the flagellum on the antero-ventral margin, but more on the postero-dorsal, so some flexibility between the pedicel and flagellum is possible, although limited in the anterior direction by the prolongation of the pedicel. During copulation the male clasps the female around the top of the abdomen from underneath (Werneck, 1936; Sikora & Eichler, 1941), the pedicel and flagellum being curved to match the curvature of the abdomen. The antennae are raised above the head of the male and the intrinsic adductor muscles contracted. The pedicel and flagellum are thus brought down over the abdomen of the female, the flagellum being constrained by the form of its junction with the pedicel. The form of the pedicel-flagellum joint is such that, should the haemolymph pressure be reduced, the joint membrane would collapse and further contract the flagellum against the female. However, lice are not known to have control over haemolymph pressure in their antennae, although larvae of Lepidoptera are known to control their antennal movement partially by this means (Matsuda, 1965). The mechanical strength and degree of possible control of a system involving joints as described above is likely to be inversely proportional to the number of joints in succession, with a single joint being the most efficient. The degree of curvature attainable using three segments is sufficient to grasp the female. For these reasons only the first flagellomere is required to take on a clasping function; the apical two flagellomeres may be retained in a sensory capacity (most Ischnocera) or lost (Trichodectidae). In Trichodectidae the last two flagellomeres have contracted and fused to the first flagellomere in all males (although a small semicircular sclerotisation, probably representing the apical flagellomere, is present in the male of *Eurytrichodectes paradoxus*) and in females of the Neotrichodectinae, Trichodectinae, Bovicolinae and most Eutrichophilinae. The sensilla of the two apical flagellomeres are retained on the remaining flagellomere.

The firmness with which the female is held may be increased by projections in the form of spikes or denticles on the antennae, particularly on the flagellum. Trichodectidae are characterised by the possession of two modified setae apically on the male flagellum, which take the form of sharp, stout teeth (Fig. 13).

Trichodectidae have two sensilla coeloconica and three sensilla placodea on the terminal flagellomere, sometimes closely associated (Clay, 1970; Kim & Ludwig, 1978). In *Loricicola malaysianus* and *L. mjobergi* the sensilla are in pits with tongue-like projections around them.

Thorax

Figures 17 and 18 depict a generalised trichodectid thorax, labelled with the terms used in this study. In all Trichodectidae the rhombic sclerite anterior to the pronotum is present; the pronotum itself generally bears two lateral sclerites, sometimes narrowly joined medially. The mesonotum and metanotum are fused, with prominent pleural ridges extending onto them; there may, as with the pronotum, be a medial zone of desclerotisation. Contrary to the assertion of Mayer (1954), the lateral cervical sclerite is always present and bears two anterior setae. The pronotum is fused to the propleuron, which in turn is fused to the prosternum. The prosternum may extend anteriorly between the fore-coxae and be unsclerotised medially. The mesosternite, fused to the prosternite, may also be medially divided. The mesepisternum is difficult to delimit, but rarely extends unbroken between the metasternite and the metanotum. The metasternite, if present, is only rarely fused to the mesosternite, and is never sclerotised medially. Posterior to



Figs 17, 18 Diagrammatic representations of generalised trichodectid thorax, with terms used in this study. 17, dorsal. 18, ventral.

the metacoxa may be a semicircular sclerite ('postcoxale' of Matsuda, 1970). In *Procavicola* (*Meganarionoides*) this is very heavily sclerotised and fused to abdominal pleurum II; the two postcoxales may also fuse medially.

One, two or three setae are always present medially on the anterior margin of the thorax posterior to the temple margin of the head. The lateral margins of the thorax also bear setae, which may be more or less abundant. A row of setae is generally present across the posterior dorsal margin of the prothorax and pterothorax, sometimes interrupted medially ('median gap'). Setae are sometimes present on the dorsal disc of the prothorax and pterothorax ('anterior setae'), and medially on the mesosternum.

The legs of Trichodectidae, in common with those of most other mammal lice, terminate in a single tarsal claw. In most species this claw is smooth ventrally, but it is toothed ventrally in *Dasyonyx* (Figs 14, 15) and ridged in *Eurytrichodectes* (Fig. 16). In many species a small hyaline projection, which may be pointed or blunt (Figs 14, 15), is present at the base of the claw. Mayer (1954), in her study of *Bovicola caprae*, terms this structure a 'pulvillus' but, as a true pulvillus is generally paired (Richards & Davies, 1977; Chapman, 1982), this term is inappropriate. The projection is more probably an empodium or arolium, or even a simple basal tooth of no wider homology. Kim & Ludwig (1978, 1982) maintain that the pulvillus and empodium do not occur in the Phthiraptera, but Clay (1969) demonstrates the presence of an empodium in Menoponidae (Amblycera), and Clay (1970) figures structures in *Boopia* (Amblycera) that almost certainly are pulvilli, although she follows K  ler (no reference given) in terming them euplantulae (plantulae) of the second tarsomere.

Abdomen

In this study the 'true' segment number is referred to by roman numerals to distinguish it from the apparent number. The terms 'sternite', 'pleurite' and 'tergite' are used for the sclerites of the sternum, pleurum and tergum respectively of each segment.

Segment I is represented in Trichodectidae by the reduced tergum I only. In this respect the family is similar to the Trichophilopteridae, but differs from all other Ischnocera, in which segment I is absent.

Segments III–VIII bear the spiracles, if these are present; spiracles are never present on segments I and II. Within the Trichodectidae many species have fewer than the plesiomorphic number of six pairs of abdominal spiracles (Table 1). Loss has apparently taken place sequentially from the posterior, so that if any spiracles are present one pair is on segment III, and if more than one pair is present there are no intercalating segments which lack spiracles between those segments with spiracles. There is, however, no evidence that spiracles have necessarily been lost one pair at a time. Whilst in *Procaivicophilus* (*Meganarionoides*) *angolensis*, *P. (M.) colobi* and *P. (M.) baculatus* the posterior pair of spiracles only is very small and apparently in process of being lost, in *Loriscicola* (*L.*) *hercynianus* and *L. (L.) siamensis* the posterior two pairs are extremely small, probably non-functional, and apparently in process of being lost. In a number of clades, sister-groups exhibit multiple discontinuities in spiracle number. The sister-species *Loriscicola* (*L.*) *mjoeberti* and *L. (L.) malaysianus* have six and zero pairs respectively; *Felicola viverriculae* and an undescribed sister-species have three and zero pairs respectively; the *Loriscicola* (*P.*) *lenicornis* – *wernecki* clade and the sister *L. (P.) acuticeps* – *neoafricanus* clade have four and zero pairs respectively. Variation within species can occur, although it is generally erratic. *Felicola subrostratus* normally has three pairs of abdominal spiracles; the species is widespread and found on many hosts, but on Madagascar, where the host is *Eupleres goudoti*, there may be three or two pairs, and specimens exhibiting asymmetry are present in the British Museum (Natural History) collection. Asymmetry has also been noted in *Trichodectes emeryi*, one paratype of which has six spiracles on one side of the abdomen and five on the other. *Trichodectes* (*S.*) *potus* is unusual in that the female has three pairs of abdominal spiracles and the male only two, the only known example in the lice of sexual dimorphism in spiracle number.

Most Trichodectidae have either six, three or no pairs of abdominal spiracles, other numbers

TAXA	NUMBER OF PAIRS OF SPIRACLES
<i>Geomydoecus</i> , <i>Neotrichodectes</i> , <i>Felicola</i> (F.) <i>helogale</i> , <i>F.</i> (F.) <i>hopkinsi</i> , <i>F.</i> (S.) <i>fahrenheiti</i> , <i>F.</i> (S.) <i>guinlei</i> , <i>Loriscicola</i> (L.) <i>malaysianus</i> , <i>L.</i> (P.) <i>paralaticeps</i> - <i>mungos</i> clade, <i>L.</i> (P.) <i>acuticeps</i> - <i>neoafricanus</i> clade	0
<i>Felicola</i> (S.) <i>bedfordi</i>	1
<i>Felicola</i> (F.) <i>subrostratus</i> from <i>Eupleres</i> , <i>Trichodectes</i> (S.) <i>potus</i> ♂	2
<i>Felicola</i> (F.) all species except <i>helogale</i> and <i>hopkinsi</i> , <i>F.</i> (S.) all species except <i>bedfordi</i> , <i>fahrenheiti</i> and <i>guinlei</i> , <i>Trichodectes</i> (S.) <i>fallax</i> , <i>T.</i> (S.) <i>octomaculatus</i> , <i>T.</i> (S.) <i>potus</i> ♀	3
<i>Loriscicola</i> (P.) <i>bengalensis</i> - <i>jucii</i> clade, <i>L.</i> (P.) <i>aspidorhynchus</i> , <i>L.</i> (P.) <i>sumatrensis</i> , <i>L.</i> (P.) <i>lenicornis</i> , <i>L.</i> (P.) <i>wernecki</i>	4
<i>Trichodectes</i> (<i>Paratrichodectes</i>)	5
<i>Trichodectes</i> (T.), <i>T.</i> (S.) all species except <i>fallax</i> - <i>potus</i> clade, <i>Werneckodectes</i> , <i>Neolutridia</i> , <i>Lutridia</i> , <i>Protellicola</i> , <i>Loriscicola</i> (L.) all species except <i>malaysianus</i> , <i>Dasyonyginæ</i> , <i>Eutrichophilinae</i> , <i>Bovicolinae</i>	6

Table 1 Distribution of number of pairs of abdominal spiracles in the Trichodectidae.

being less common (Table 1). From the cladogram, reduction to five, four and one pair can be seen to have occurred once, reduction to two and three pairs twice, and reduction to none eight times. The loss of abdominal spiracles plainly cannot be used *a priori* as a taxonomic character defining (holophyletic) genera, as proposed by Ewing (1936), but neither is it as variable as suggested by Kéler (1938a) and Hopkins (1941), who treat it as a character of specific value only. The selective advantage of this reduction is not known, but it may be an adaptation to exclude dust from the tracheal system, or to reduce water loss.

A posterior commissure joining the two main abdominal tracheal trunks is present in Anoplura, Rhyncophthirina, Boopiidae and Trimenoponidae (Amblycera), Philopteridae (Ischnocera) and 'some Trichodectidae' (Harrison, 1915; Ferris, 1931). All species of Trichodectidae examined in this study possess a posterior commissure, which is consequently assumed to have a universal distribution throughout the family. The presence of the posterior commissure is assumed to be plesiomorphic for the Phthiraptera (Clay, 1970).

In all lice segment IX is the genital segment, and the male genitalia open to its posterior and the female genitalia to its anterior. Modifications of this segment are discussed in detail below.

In both sexes of Trichodectidae segments X and XI are fused. In females segment XI lies caudally, posterior to X, but in males the modifications of segment IX have led to the displacement of both X and XI onto the dorsal surface of the abdomen. Most male Trichodectidae have the genital opening posterior or postero-dorsal. The postgenital segments are reduced to form a small anal cone arising from the dorsal (anterior) wall of the genital chamber (Kéler, 1957) (Fig. 19).

Conical projections are present either dorsoposteriorly or ventroposteriorly on the first three

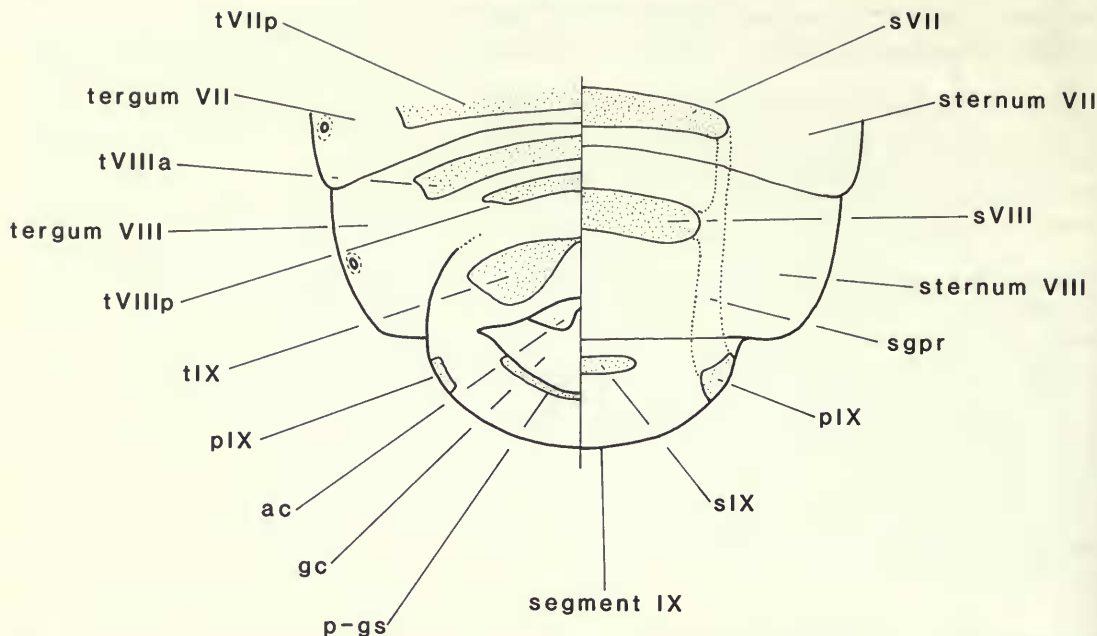


Fig. 19 Diagrammatic representation of terminal segments of trichodectid male abdomen, with terms used in this study. t – tergite; s – sternite; p – pleurite; ac – anal cone; gc – genital chamber; p-gs – post-genital sclerite; sgpr – lateral rods of subgenital plate.

pleura (II, III and IV) in many Trichodectidae. The distribution of the pleural projections is summarised in Table 2.

Male Trichodectidae, alone among Phthiraptera, possess 'lateral abdominal flecks', first noted in *Werneckiella* by Moreby (1978). The flecks are small pits positioned on the anterodorsal angles of pleura III–VII, occasionally on II and VIII, and anterolaterally on terga III–V in many species (Fig. 218). In *Werneckiella* there are small sclerites situated anteriorly and posteriorly of the pit; in *Trichodectes canis* there are no sclerites bordering the pit but a small sclerite is present at its base; in *Neotrichodectes* there are no sclerites associated with the pit at all. The function of these structures is unknown.

In some species of Phthiraptera terga II and/or III of the males are ornamented with large setae or projections. Such developments are numerous in the Trichodectidae. Many species of *Felicola* have a pair of long setae medially on male tergum II (Figs 180, 187, 188), whilst *Geomydoecus* (*Thomomydoecus*) spp., *Trichodectes ovalis*, *T. ugandensis* and an undescribed subspecies of *T. galictidis* have paired 'combs' of long setae on male terga II and III (Fig. 161), and *Bovicola multispinosa* and *B. hemitrangi* have paired semicircular 'brushes' of setae on male tergum II (Fig. 41). *Damalinia ornata* has sclerotised blunt projections on male terga II and III. These specialised setae and projections may in some way assist the male to hold the female during copulation, although in no case have the setae or projections been observed to be damaged, as they might be expected to be should they operate against the female abdomen, and there is no observational evidence to support the hypothesis.

Males of *Neotrichodectes* species have a pair of small median setae on terga II–VII, sometimes separated by a seta of normal length (Fig. 229). This feature, not found in females or males of any other group, is of unknown function.

Female genitalia

The female subgenital plate of Trichodectidae comprises either sternite VIII or sternites VIII and VII fused. The posterior margin of sternum VIII forms the ventral margin of the vulva. In many species the margin is expanded posteriorly and slightly laterad (Fig. 94), and in others the

TAXA	SEX	PLEURUM	PLEURUM	PLEURUM
		I I	III	I V
		D V S	D V S	D V S
<i>Neotrichodectes mephitidis</i>	♀			+
<i>Cebidicola</i>	♂ ♀			+ +
<i>Procavicola</i> - <i>Eurytrichodectes</i> clade, <i>Loriscicola mjoeberti</i> , <i>Felicola seylonicus</i> - <i>viverriculae</i> clade	♂ ♀			+ + +
<i>Felicola bedfordi</i> , <i>F. congoensis</i> , <i>F. cooleyi</i> , <i>F. cyniotis</i> , <i>F. decipiens</i> , <i>F. helogale</i> , <i>F. minimus</i> , <i>F. liberiae</i> - <i>subrostratus</i> clade, <i>Loriscicola aspidorhynchus</i> , <i>L. caffra</i> , <i>L. felis</i> , <i>L. hercynianus</i> , <i>L. malaysianus</i> , <i>L. mungos</i> , <i>L. spenceri</i> , <i>L. sumatrensis</i> , <i>L. wernecki</i> , <i>L. bengalensis</i> - <i>juccii</i> clade	♂ ♀			+ +
<i>Loriscicola acuticeps</i> , <i>L. africanus</i> , <i>L. lenicornis</i> , <i>L. neoafricanus</i>	♂ ♀			+ ?
<i>Felicola occidentalis</i> , <i>F. quadraticeps</i> , <i>F. vulpis</i>	♂ ♀		+	+
<i>Felicola calogaleus</i> , <i>F. setosus</i>	♂ ♀		+ +	+ +
<i>Trichodectes xorillae</i>	♂ ♀	+ + + +	+ + + +	+ + ?
<i>Geomydoecus</i> (G.) most species	♂ ♀	+	+	+ +
<i>Geomydoecus</i> (G.) <i>thomomys</i> - <i>dakotensis</i> clade	♂	+ +	+ +	+ +
<i>Geomydoecus</i> (<i>Thomomydoecus</i>)	♀	+ +	+ +	+ + +

Table 2 Distribution of abdominal pleural projections in the Trichodectidae. For pleura II, III and IV an indication is given whether a dorsal ('D') or ventral ('V') projection is present, and whether those projections are sclerotised ('S'). In each case the presence state is indicated by '+'. Very light sclerotisations are indicated by '?'.

centre of the margin is greatly expanded into a flat lobe termed the 'subgenital lobe' (Figs 149, 153, 175). The subgenital lobe appears to have evolved at least three times in the Trichodectidae, and its form is of taxonomic and systematic value. Its function, however, is not known.

To each side of the vulva is a projection from sternum VIII, the gonapophysis of segment VIII (Lyal, in prep., *b*). The structure of this is variable. In all cases a basal internal apophysis is produced, presumably as a muscle attachment (Kéler, 1938a). The gonapophysis lies longitudinally, parallel to the abdomen; it may curve onto the dorsal surface apically. It may be long, slender and apically acute (Fig. 235), long and apically rectangular (Fig. 154), broad and membranous (Fig. 243), produced into a rounded, toothed or rectangular medial lobe with an apical 'spur' (Figs 175, 233, 236), with the spur reduced (Fig. 237) or absent (Fig. 211), sometimes with serrations laterally (Fig. 211). Setae may be present on the gonapophyses and the ventral vulval margin in various configurations, occasionally arising from sclerotised tubercles. In some cases a sclerotised band links the gonapophyses and the vulval margin, but in most cases this is not present and the connection is membranous.

The curvature of the gonapophyses about both longitudinal and lateral axes produces a complex three-dimensional structure difficult to interpret on slide-mounted specimens. The orientation of the gonapophysis may be altered by pressure of the coverslip during mounting, especially if it has a membranous base. In addition, differences in orientation, either

natural or caused by the mounting process, may give the impression of very different shapes.

Observations by Ferris (1951) and Murray (1957*a*, 1957*b*) indicate that the gonapophyses are used, at least in some species, to trap the hair on which the egg is to be laid, guide the egg onto it, and mould the attaching cement. For *Bovicola ovis* the diameter of the hair is of importance in determining whether the egg will be laid (Murray, 1957*b*) and this is almost certainly detected by the gonapophysis. There is thus selection pressure on the form of the gonapophysis relating to the structure of the host hair.

Posterior to the vulva and sometimes covered by the subgenital lobe is the 'sub-vulval area', which sometimes bears characteristic spines or scales.

Also posterior to the vulva is a single sclerite which, as it cannot be homologised with either the gonangulum or sternite IX + X (Lyal, in prep., *b*), is termed the 'post-vulval sclerite' (Moreby, 1978). This sclerite may be single, medially divided, narrow and strip-like, broad and triangular, fused to the postgenital pleurite, or absent (Figs 154, 175, 236, 237, 243).

The female genital chamber, opening at the vulva, is oval, dorso-ventrally compressed, and lightly-sclerotised. The dorsal wall of the chamber may be heavily sculptured and bear sclerotised spicules, ridges or spines; this sculpturing may extend on to the postgenital sterna. The ventral wall may be similarly sculptured, although usually to a lesser extent; where the subgenital lobe is present the sculpturing of the genital chamber may extend onto its dorsal surface. The sculpturing of the walls of the chamber probably provides a highly frictional surface against which the spicular surface of the endophallus acts to provide a firm union during copulation. The nature of the sculpturing and the distributions of spicules or spines may be taxonomically useful at the specific or subspecific level. The common oviduct opens into the anterior end of the genital chamber and curves sharply posteriad to lie dorsally to the chamber. Dorsal to the vulva the common oviduct curves sharply anteriad and divides into the two paired oviducts (Fig. 20). The genital chamber, although assuming a more or less circular cross-section during the passage of an egg and perhaps during copulation, is, when at rest, a dorso-ventrally

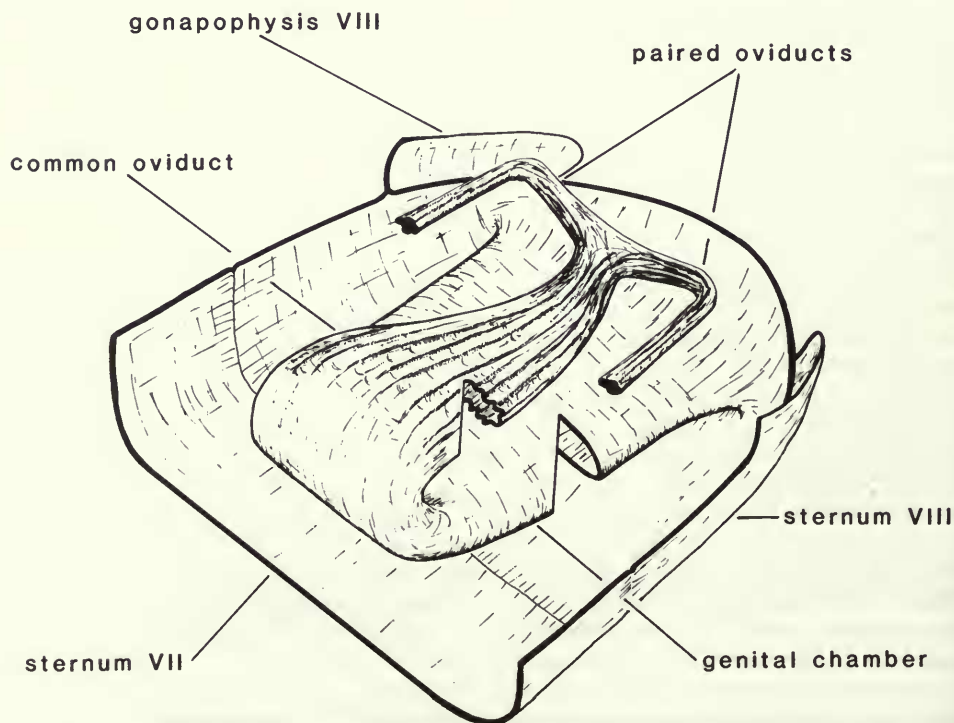


Fig. 20 Diagrammatic three-dimensional representation of trichodectid female genital chamber and oviducts (internal), with terms used in this study.

flattened, fairly rigid structure, the minimum width of which is governed by the diameter of the egg. The oviduct, however, is an elastic, folded membranous tube, compressed and folded to reduce volume, and expanding only to allow passage of the egg. The common oviduct must, at the junction with the genital chamber, be the same diameter as the chamber. At its division into the paired oviducts, however, it is narrow and greatly folded when at rest. Between these two points it narrows more or less abruptly, and folds may be apparent in its walls. Price & Emerson (1971) interpret these folds in *Geomydoecus* as striations of the dorsal wall of the genital chamber, and term this apparently membranous structure the 'genital sac'. The true dorsal wall is interpreted as the ventral wall and the true ventral wall is apparently not observed. The form of the folds of the 'genital sac' (common oviduct), as well as its length and the width of its junction with the genital chamber, have been utilised by Price and his co-workers as specific and subspecific characters in their revisionary work on *Geomydoecus* (e.g. Price, 1974; Price & Emerson, 1971; Price & Hellenenthal, 1976; Timm & Price, 1980). The apparent constancy of the dimensions of the oviduct is related to the size of the egg and perhaps to the restrictions in variability of size of the genital chamber imposed by selection. The apparent constancy of the folds is more puzzling although it is possible that tubes of identical length and diameter have an optimum folding pattern if compressed in the same way. The wall of the common oviduct may also be lightly sclerotised, at least near to the junction with the genital chamber. The folds of the common oviduct have not been utilised as a taxonomic character elsewhere in the Phthiraptera.

Blagoveshtchenski (1956) examines several species of Trichodectidae but fails to find evidence of a spermatheca in the family. In this study examination of slide-mounted specimens of most species has failed to reveal a spermatheca in any genus apart from problematically in *Dasyonyx*, where a lightly-sclerotised sac, differing in form between species, is developed from the wall of the common oviduct. The relatively anterior position of this sac in comparison to the spermatheca of other Phthiraptera suggests that the two structures are not homologous. No histological or anatomical studies have been carried out on the sac.

The male abdomen and copulation

The opening of the male genital chamber ('genital opening') is always posterior to sternum IX, and primitively in the lice is ventrally positioned and distant from the anus, which is terminal. During copulation the male and female are usually oriented the same way, with male ventral to female. The tip of the male's abdomen is curved dorsally and anteriorly so that the genital openings of the male and female meet. The male genitalia consequently enter the female genital chamber 'upside-down', with the ventral side of the former coming into contact with the dorsal wall of the latter. Should sclerotised tergites be absent (as in *Neotrichodectes* and *Geomydoecus*) or greatly reduced (as in *Trichodectes galictidis* and *Felicola*) flexion of the male abdomen during copulation is evenly distributed along the membranous dorsal surface. If sclerotised tergites are present and fully-developed, however, flexion must be about the sclerite-membrane-sclerite joints of the dorsal surface, these thus functioning as 'hinges'. At each such hinge, there will be considerable deformation of the internal structures during flexion, whilst between the hinges there will be no deformation. Increasing the number of hinges on the dorsal surface permits smoother curvature of the abdomen and reduces the internal deformation at each hinge. Many male Trichodectidae have tergal sclerites divided into an anterior and a posterior plate on at least some segments (Figs 103, 105, 136), possibly for this reason. The degree of internal deformation may be further reduced by modification of the shape of the plates. The form of plate which, when placed in series, causes maximum internal deformation and requires maximum membrane area: sclerite area ratio for flexion is a simple rectangle, with anterior and posterior margins at right angles to the long axis of the abdomen. These factors can be diminished by introducing curvature in the anterior and posterior margins of the plates, either with both margins parallel or opposite, producing a series of alternating biconvex and biconcave plates (Lyal, 1983). Both these patterns are approached in the Trichodectidae (Figs 68, 103, 105). The flexibility required of the ventral surface of the abdomen is developed, should the sterna be

sclerotised, by increasing the lengths of the sclerites and allowing them to overlap when the abdomen is at rest (Figs 103, 105).

Despite the increased flexibility of the abdomen achievable by modifications of the tergal and sternal plates, the position taken by the male during copulation is compatible with a ventral genital opening only if the abdomen is long and slender. A short, broad abdomen will not deform sufficiently to turn back on itself and bring the male genital opening into contact with the vulva. Such a short, broad abdominal form has been developed several times in the Phthiraptera, however, including at least once in the Trichodectidae. In most cases the limitation imposed on the degree of curvature of the abdomen has been met by a posterior or even dorsal migration of the genital opening, thus reducing the degree of curvature necessary. This displacement has been effected by an increase in length of sterna VII, VIII and IX and a concomitant shortening of the corresponding terga. In Trichodectidae this may lead to the division of tergite VIII longitudinally by segment IX (Fig. 212). The re-positioning of the genital opening has increased its proximity to the anus, and in Trichodectidae the anus is contained within the genital chamber with the reduced segments X and XI projecting from the genital opening (Fig. 19). The curvature required of the abdomen has been further limited in some Trichodectidae by two distinct adaptations. In some species of *Felicola* segment IX is developed into a long, slender posterior process and the genital opening is dorsal and apical (Fig. 187). The basal apodeme and parameres are elongate and slender (Fig. 205). Most of the curvature required is probably developed at the base of segment IX and the junction of the parameres and the basal apodeme. Constriction of the endophallus at the latter fold is prevented by the presence of a reduced, circular mesomeral arch, lacking an extension, which, being fused to the endophallus, prevents the structure from being pinched shut. In some *Loricicola* species segment IX projects dorsally from segment VIII, the genital opening being dorsal (Fig. 114). This positioning limits the degree of curvature required of the abdomen by increasing the proximity of the genital opening to the vulva on minimum curvature.

Male terminalia

In Trichodectidae the subgenital plate is fundamentally uniform in construction, although great superficial differences may exist between species. The plate is here considered to comprise eight discrete elements: sternites VII, VIII, IX (and, occasionally, VI); a pair of rods (referred to as 'subgenital plate rods' or 's.g.p.r.' in this study) which lie laterally to the sternites and sometimes fuse them together (Figs 19, 165, 212); the two pleurites of segment IX, and the post-genital sclerite, which is of uncertain homology (Fig. 19). Any of these elements may be present, reduced or absent, or fused to adjacent sclerites. The sternites and the post-genital sclerite may be whole or medially divided. In cases of extreme reduction only the lateral rods may be left (Fig. 163) or all the sclerites absent (Fig. 187). In the most complete form (Fig. 68), all the sclerites are fused, forming a squared plate; usually there are membranous areas surrounding the sternal setae ('perisetal gaps'), but these may be absent (Fig. 115).

The subgenital plate rods on sternum VIII are always connected to the ventral wall of the genital chamber in Trichodectidae, a feature also observed in some Anoplura. The function of this attachment is not known, although in species with ventrally-positioned parameres and a median posterior extension to the mesomeral arch, the difference in lengths between the dorsal wall of the genital chamber and the membrane between the basal apodeme and the subgenital plate might cause divergence of the apices of the parameres and mesomeral arch extension during extrusion of the genitalia to allow eversion of the endophallus.

In some Trichodectidae the posterolateral angles of the subgenital plate are greatly extended into setose lobes termed 'styli' by Eichler (1963) (Figs 46, 68). Abdominal sternal sclerites are probably derived from a fusion of the sternal plate and the coxal elements of the paired abdominal appendages (coxopodites) (Matsuda, 1976; Richards & Davies, 1977). In the subgenital plate of the Acercaria the paired nature of the gonocoxopodite component may be expressed as a concavity of the posterior margin of the plate and concomitant projection of the posterolateral angles (Matsuda, 1976). True abdominal styli are derived from the paired

abdominal appendages and are serially homologous with either the shaft of the thoracic legs or the coxal styli (spurs of Matsuda, 1976) of the thoracic legs as present in the Machilidae (Thysanura) (Matsuda, 1976; Richards & Davies, 1977). Styli are not, therefore, homologous with the coxopodites, but arise from them, being separated by a clear sulcus. Although true styli are present in some Psocoptera (Matsuda, 1976), the posterior extensions of the subgenital plate of Trichodectidae are not demarcated by a sulcus and thus are not homologous with true styli. The so-called styli of the Trichodectidae are an indication of the gonocoxopodite component of the subgenital plate, and are here termed 'pseudostyli'. Taxonomic use may be made of the form of the pseudostyli, which is very variable in the Trichodectidae, but the difficulty of assigning polarity to transformation series limits the applicability of this character within phylogenetic studies. The distribution of the pseudostyli through the Trichodectidae, however, is utilised in the construction of the phylogeny of the family (see below).

Male genitalia

The structure of the male genitalia of lice and the homologies of the major parts are discussed by Lyal (1983 and in prep., *b*). The genitalia consist of a more or less sclerotised basal apodeme supporting caudally a pair of parameres which may be fused ventrally and a pair of mesomeres which may be fused dorsally; fused to the interior faces of the parameres and mesomeres is the permanently-everted portion of the eversible endophallus (Lyal, 1983 and in prep., *b*). In most Trichodectidae both parameres and mesomeres are present, the latter usually being fused apically (Figs 170, 198), the fused portion generally being extended posteriorly (Fig. 224). The parameres may also be fused, forming a median ventral plate (Fig. 250). The parameres and mesomeres may meet the basal apodeme together (Fig. 170) or separately (Fig. 250). The full range of variation of the male genitalia is discussed in the character analysis and taxonomy sections below.

During copulation the endophallus everts into the female genital chamber. As described above, the interior of the femlae genital chamber is roughened and lined with scales. The endophallus is likewise roughened, being covered with small chitinous spicules or larger sclerites. The probable function of this adaptation is to maintain a firm connection between the male and female genitalia during copulation. The form of the endophallus and the distribution of the spicules and sclerites are species-specific and very variable, possibly functioning as pre-zygotic isolating barriers.

Character survey

As noted above, the characters and character states listed below were selected from a much larger set of characters and states. In some cases reasons for rejection are discussed below. The full list of characters and the complete data matrix are presented in Lyal (1983) and are deposited in the library of the British Museum (Natural History).

1	Posterior of basal apodeme lateral struts ('b.a.l.s.')	symmetric in vertical plane asymmetric in vertical plane (Figs 193, 195)	0 1		g
2	Anterior end of basal apodeme	flat, convex, concave (Figs 91, 200, 250) deeply concave (Fig. 52) acuminate (Fig. 173)	0 1 1'		g g
3	Posterior bifurcation of b.a.l.s.	absent present (Fig. 173)	0 1		g
4	Posterior of b.a.l.s.	lacking lateral extension with lateral extension to mesomeres (Fig. 239)	0 1		g
5	Anteposterior spur of b.a.l.s.	absent present (Fig. 83)	0 1		g

6	Shape of basal apodeme	not long and 'waisted'	0	
		very long, with median 'waist' (Fig. 119)	1	g
7	Posterior of b.a.l.s.	not modified as below	0	
		broad and obtuse in meeting parameres (Fig. 198)	1	g
8	Posterior of b.a.l.s.	not modified as below	0	
		sharply inturned and convex (Fig. 200)	1	g
9	Posterior of b.a.l.s.	not modified as below	0	
		incurred to parameres (Figs 144, 145)	1	g
10	Basiparameral sclerites	absent	0	
		present, fused to parameres	1	g
		present, free	2	g
11	Paramere fusion	not fused to mesomeral arch	0	
		fused to mesomeral arch in part (Figs 60, 75)	1	g
		completely fused to mesomeres (Fig. 74)	2	g
12	Paramere fusion	not fused to basal apodeme	0	
		fused exteriorly to basal apodeme (Fig. 75)	1	g
		fused medially or completely to basal apodeme (Figs 145, 172, 174)	1'	g
13	Paramere fusion	not fused together or closely associated	0	
		fused together	1	g
		not fused but closely associated, with line of division apparent (Figs 223, 224)	1'	g
14	Parameral apices	unfused	0	
		fused	1	g
15	Paramere shape	not as described below	0	
		fused to shield-shaped plate (Figs 239, 242)	1	g
16	Paramere shape	not as described below	0	
		fused as described in character 15, with antero-median projection (Fig. 238)	1	g
17	Parameral plate shape	not as described below	0	
		produced apically into incurving points (Fig. 171)	1	g
18	Parameral orientation	similar	0	
		at right-angles to each other (Fig. 170)	1	g
19	Paramere shape	more or less broad, thick	0	
		very thin, deflected asymmetrically (Fig. 174)	1	g
20	Paramere shape	more or less broad	0	
		narrow rods (Figs 196, 197)	1	g
21	Paramere shape	not as described below	0	

		very broad, lanceolate, scoop-shaped (Fig. 172)	1	g
22	Median internal projection of parameres	absent	0	
		present	1	g
23	Paramere size	large or moderate	0	
		small discs (Fig. 84)	1	l
24	Paramere shape	not as described below	0	
		cylindrical (Figs 169, 205)	1	g
25	Paramere shape	not as described below	0	
		basally very narrow, medially broad (Fig. 198)	1	g
26	Paramere shape	not as described below	0	
		with characterically- differentiated base and blade (Fig. 51)	1	g
27	Base of parameres	not as described below	0	
		broad, club-like (Fig. 192)	1	g
		block-like (Fig. 201)	1'	g
		cuboid (Fig. 52)	1"	g
28	Base of parameres	lacking flange	0	
		with flange (Fig. 118)	1	g
29	Paramere and mesomere shape	not as described below	0	
		of characteristic asymmetric form (Fig. 249)	1	g
30	Reduction of parameres and mesomeres	not reduced as below	0	
		characteristically reduced (Fig. 52)	1	l
		characteristically greatly reduced (Fig. 53)	2	l
31	Mesomeres	present	0	
		absent	1	l
32	Mesomeral position	reach or fail to reach		
		b.a.l.s.	0	
		extend mesad of b.a.l.s.	1	g
33	Mesomere fusion	apically fused to form arch	0	
		not apically fused	1	l
34	Lateral desclerotisations of mesomeral arch	absent	0	
		present (Fig. 118)	1	g
35	Lateral flexions of mesomeral arch	absent	0	
		present (Figs 107, 225)	1	g
36	Mesomeral arch	not as described below	0	
		modified into tripartite arch (Fig. 93)	1	g
37	Mesomeres basally, between b.a.l.s.	not modified as below	0	
		sharply directed posteriad (Fig. 224)	1	g
38	Mesomeral arch mesally	smooth or with projection	0	
		with two nipples (Fig. 221)	1	g
39	Diameter of mesomeral arch	less than half the length of the permanently-everted endophallus	0	
		more than half the length of the permanently-everted endophallus	1	g

		as great as the length of the permanently-everted endophallus	2	g
40	Shape of mesomeral arch	not as described below with median anterior deflection (Figs 191, 192)	0	
41	Shape of mesomeral arch	circular or elliptical	0	g
		rectangular (Fig. 198)	1	g
42	Shape of mesomeral arch	not as described below extension lost, arch 'looped' (Fig. 247)	0	
			1	g
43	Shape of mesomeral arch	not as described below widely circular (Fig. 55)	0	
			1	g
44	Shape of mesomeral arch	not as described below pentagonal, convex distally (Fig. 62)	0	
			1	g
45	Shape of mesomeral arch	smoothly curved sharply inturned to parameres (Fig. 81) extending anteriorly to posterior end of basal apodeme and sharply recurved (Figs 82, 219)	0	
			1	g
46	Shape of mesomeres	not as described below very slender, string-like (Fig. 52)	2	g
			0	
47	Median extension of mesomeral arch	present	1	g
		absent	0	l
48	Apex of mesomeral arch extension	not bifurcate	1	
		bifurcate	0	g
49	Shape of mesomeral arch extension	not as described below broadly expanded, lanceolate	0	
			1	g
50	Tongue-like sclerite between parameres	absent	0	
		present	1	g
51	Everted part of endophallus	not sclerotised	0	
		sclerotised	1	g
52	Endophallus spiculation	not as described below numerous 'V'-shaped rods	0	
			1	g
53	Endophallus spiculation	not as described below comprising large hook-like spines (Fig. 107)	0	
			1	g
54	Endophallus spiculation	not concentrated about gonopore	0	
		concentrated about gonopore with dense 'V'-shaped patch about gonopore	1	g
			2	g
55	Endophallus spiculation	not as described below including median row of hook-like scales	0	
			1	g
56	Endophallus spiculation	not as described below dense and refrigent in part	0	
			1	g
57	Gonapophysis setae	present	0	
		absent	1	l
58	Gonapophysis setae	lacking sclerotised tubercles	0	

		some having sclerotised basal tubercles (Fig. 150)	1	g
59	Gonapophysis setal tubercles	absent, or present and not characteristically fused	0	
		present and characteristically fused (Fig. 111)	1	g
60	Gonapophysis setal tubercles	absent, or present and in characteristic pattern (Fig. 153)	0	
		present and modified from characteristic pattern by loss of apical non-tuberculate seta (Fig. 146)	1	l
61	Gonapophysis shape	not as described below	0	
		spoon-shaped (Fig. 156)	1	g
62	Gonapophysis shape	not as described below	0	
		hook-shaped (Fig. 66)	1	g
		hook-shaped with spur (Fig. 67)	1'	g
63	Gonapophysis shape	not explanate ventrally (other than as discrete lobe)	0	
		thinly explanate ventrally (other than as discrete lobe)	1	g
64	Gonapophysis lobe	absent	0	
		present	1	g
65	Apex of gonapophysis	acute or obtuse	0	
		not projecting beyond lobe (if present); apparently absent	1	l
66	Gonapophysis lobe	not very thick	0	
		very thick	1	g
67	Gonapophysis lobe	absent, or not as described below	0	
		broad, formed of fused tubercles (Fig. 233)	1	g
68	Gonapophysis lobe	absent, or not as described below	0	
		narrow, rectangular, formed from 2 or 3 fused tubercles (Fig. 177)	1	g
69	Gonapophysis lobe	negative for character 67	0	
		or, if positive, flattened	0	
		positive for 67 and folded anteriorly	1	g
		positive for 67 and greatly folded	2	g
70	Gonapophysis lobe	absent, or not as described below	0	
		produced into spines posteriorly (Fig. 211)	1	g
71	Gonapophysis junction with ventral vulval margin	acute	0	
		smoothly continuous	1	g
72	Ventral vulval margin	unsclerotised	0	
		sclerotised	1	g
73	Ventral vulval margin	no shorter than length of gonapophyses	0	

		shorter than length of gonapophyses (Fig. 102)	1	g
74	Ventral vulval margin	lacking setal tubercles with setal tubercles (Fig. 156)	0	
			1	g
75	Ventral vulval margin	not expanded	0	
		expanded (Figs 94, 126)	1	g
76	Ventral vulval margin	not as described below	0	
		greatly produced and rounded (Fig. 113)	1	g
77	Ventral vulval margin	not as described below	0	
		with median narrow projection	1	g
78	Subgenital lobe	absent	0	
		present	1	g
79	Subgenital lobe margin	not serrate	0	
		serrate	1	g
		very serrate	2	g
80	Subgenital lobe surface	smooth dorsally and ventrally with overlapping pointed scales (Fig. 210)	0	
		with small spines (Fig. 208)	1	g
		with many overlapping spines (Fig. 207)	2	g
			3	g
81	Subgenital lobe, basally	lacking lateral processes	0	
		with lateral processes	1	g
82	Subgenital lobe processes (ch. 81)	not as described below	0	
		thinly sclerotised and directed posteriad	1	g
83	Subgenital lobe processes (ch. 81)	not as described below	0	
		membranous and serrate (Figs 155, 157)	1	g
84	Subgenital lobe	not bifurcate (Fig. 210)	0	
		bifurcate (Fig. 208)	1	g
85	Subgenital lobe bifurcations (ch. 84)	not as described below	0	
		rectangular, widely separate (Fig. 176)	1	g
86	Subgenital lobe	lacking submarginal setal patch	0	
		with submarginal setal patch	1	g
87	Sub-vulval area	lacking pointed scales	0	
		with pointed scales	1	g
88	Dorsal vulval face	not spinous	0	
		spinous	1	g
89	Post-vulval sclerites	present	0	
		absent	1	l
90	Post-vulval sclerites	broad, triangular	0	
		long, narrow, oriented parallel to longitudinal axis	1	g
91	Common oviduct	not as described below	0	
		with folded 'collar' at branching-point	1	g
92	Female genital chamber	lined with overlapping scales	0	

		lined with sclerotised nodules, some fused	1	g
93	Female genital chamber	not as described below with median dorsal longitudinal fold	0	
			1	g
94	Female genital chamber	not as described below with median dorsal area clear of scales	0	
			1	g
95	Female genital chamber	not as described below with median anterior dorsal area clear, thinly sclerotised	0	
			1	g
96	Female genital chamber	not as described below with spines on dorsal face	0	
			1	g
97	Female sternum VII	lacking processes with two long spikes on posterior margin (Fig. 73)	0	
			1	g
98	Reproduction	sexual	0	
		parthenogenetic	1	g
99	Male tergite VIII (if present)	with posterior element absent or, if present, not fused to tergite IX	0	
		with posterior element fused to tergite IX	1	g
100	Posterior margins of male tergum IX	not as described below greatly expanded (Fig. 79)	0	
			1	g
101	Male segment IX	without two longitudinal strengthening sclerites with two longitudinal sclerites	0	
			1	g
102	Pseudostyli	absent	0	
		present	1	g
103	Pseudostyli (if present)	not as described below broad, rounded, long (Fig. 68)	0	
			1	g
104	Pseudostyli (if present)	rounded apically angular, pointed apically (Fig. 78)	0	
			1	g
105	Male segment IX	lacking single apical projection with single apical projection (?fused pseudo- styli)	0	
			1	g
106	Male sternite VIII	not as described below characteristically enlarged (Fig. 159)	0	
			1	g
107	Male sternite VIII (if present)	not convex posteriorly characteristically convex posteriorly (Fig. 218)	0	
			1	g
108	Male perisetal gap	present	0	
		absent	1	l
109	Male sternum VI	not as described below with anterior and posterior sclerites	0	
			1	g

110	Female flagellomeres	unfused (three flagellomeres)	0	
		fused to form two flagellomeres	1	g
		fused to form one flagellomere	2	g
111	Male flagellomeres	unfused	0	
		fused	1	g
112	Male scape	greatly or slightly expanded	0	
		not expanded	1	l
113	Male scape setae	randomly scattered on posterior face	0	
		in longitudinal row on posterior face	1	g
114	Male scape setal row (if present)	numbering at least three setae on posterior face	0	
		reduced to two setae on posterior face	1	l
115	Male flagellum	lacking apical 'teeth'	1'	l
		with single apical 'tooth'	1	l
		with two apical 'teeth'	0	
		with three apical 'teeth'	1''	g
		with four apical 'teeth'	1'''	g
		with eight apical 'teeth'	1''''	g
116	Male flagellar 'teeth'	not on protuberance	0	
		on protuberance	1	g
117	Male flagellar 'teeth'	articulated basally	0	
		fused to flagellum	1	g
118	Male flagellum	lacking basal projection	0	
		with simple basal projection	1	g
		with basal projection of linked 'teeth'	1'	g
		with broad, rough, basal projection	2'	g
119	Male flagellum	not as described below	0	
		with simple median and basal projections only	1	g
120	Inner face of male flagellum	not serrate	0	
		serrate	1	g
121	Male scape	lacking apical projection	0	
		with apical projection	1	g
122	Female pedicel	lacking projections	0	
		with membranous projection	1	g
123	Male flagellum	not very long	0	
		very long	1	g
124	Flagellar sensilla placodea and coeloconica	not in pit	0	
		in pit with marginal tongue-like processes	1	g
125	Sitophore sclerite	not as described below	0	
		with posterior arms extended (Fig. 12)	1	g
126	Posterior temple angles	lacking projections	0	
		with projections (Fig. 129)	1	g
		with very long projections (Fig. 138)	2	g
127	Posterior temple margins	not as described below	0	
		produced and convex	1	g

128	Osculum	not deep deep and with characteristic anterior marginal convexity (Fig. 69)	0 1	 g
129	Pretarsus	bearing two claws bearing one claw	0 1	 l
130	Pretarsal claws	lacking ventral spines with blunt ventral spines with sharp ventral spines	0 1 1'	 g g
131	Post-coxale of leg III	not fused to abdominal pleurum II fused to abdominal pleurum II, at least in female	0 1	 g
132	Sternum II	not as described below with sclerotised apophysis articulated to pleurum II	0 1	 g
133	Atrium of thoracic spiracle	spherical tubular	0 1	 g
134	Abdominal spiracles	all of similar size spiracle VIII of male very small spiracles VII and VIII very small in both sexes	0 1 1'	 l l
135	Abdominal spiracle VIII	present absent	0 1	 l
136	Abdominal spiracle VII	present absent	0 1	 l
137	Abdominal spiracle VI	present absent	0 1	 l
138	Abdominal spiracle III	present absent	0 1	 l
139	Setae of posterior setal row of pleurum III	not stout stout	0 1	 g
140	Pleurum VII	lacking tuft of very long setae with tuft of very long setae (Figs 88, 90)	0 1	 g
141	Abdominal tergal setae	short or of medium length (Figs 105, 188) generally very long, obscuring p.l.s. (if present) (Fig. 158)	0 1	 g
142	Male tergum II	lacking specialised setae as described below with long stout setae not found on other terga (Figs 180, 188)	0 1	 g
143	Male tergum III	lacking specialised setae as described below with isolated pair of long median setae, longer than those of tergum IV (Fig. 187)	0 1	 g
144	Male terga II-IV	without specialised setae as described below each with single pair of long median setae (Fig. 182)	0 1	 g

145	Female terga I–VIII	without specialised setae as described below	0	
		each with single pair of long stout median setae	1	g
146	Female terga I–IV	with median setae	0	
		lacking median setae	1	l
147	Male terga II and III	without specialised setae as described below	0	
		with group of characteristically specialised long setae (Fig. 178)	1	g
148	Female terga I–VIII	without specialised setae as described below	0	
		each with single pair of median setae	1	g
149	Male terga II–III	without specialised setae as described below	0	
		with long setae arranged in straight rows of four or more (Figs 161, 244)	1	g
150	Male tergum II	without specialised setae as described below	0	
		with long setae arranged in curved rows (Fig. 41)	1	g
151	Postero-lateral setae	absent or possibly present but not clearly distinguished from lateral setal group	0	
		clearly present on terga II–VI	1	g
152	Male terga II–VI	with two median setae the same size as other setae of median group	0	
		with two median setae appreciably smaller than other setae of median group	1	g
153	Setae of abdominal sterna II–IV	not as described below	0	
		short, stout (Fig. 136)	1	g
154	Female abdominal setae	not as described below	0	
		very long, fine	1	g
155	Setae of male tergum II	not arising from modified sclerite	0	
		arising from very long, medially-divided sclerite	1	g
156	Abdominal setal bases	not enlarged	0	
		enlarged	1	g
157	Abdominal pleurum II	not as described below	0	
		extending narrowly onto sternum II	1	g
		extending broadly onto sternum II	1'	g
158	Dorsal projection of pleurum II	absent	0	
		present, unsclerotised	1	g
		present, sclerotised	2	g
159	Dorsal projection of pleurum IV	absent	0	
		present	1	g
160	Ventral projection of	absent	0	

	pleurum IV	present	1	g
161	Projections of pleurum IV (if present)	not as described below very long (Fig. 136)	0 1	 g
162	Male terga VI–VIII (or VI, if VII–VIII without sclerites)	not as described below with anterior sclerite longitudinally divided medially	0 1	 g
163	Male terga VI–VII	not as described below with posterior sclerite longitudinally divided medially	0 1	 g
164	Abdominal lateral flecks	absent present	0 1	 g

Character analysis

The character analysis is performed in two interconnected parts, the determination of character polarity and the construction of the cladogram. These are linked through the process of 'reciprocal illumination' (Hennig, 1966), and thus, although they are considered individually in the two sections below, there is some interaction between the two processes which will be manifested in discussion. The following two sections are intended to explain the reasons for the polarity assigned to the characters listed above, and for those groups developed in the cladogram where characters are apparently arranged non-parsimoniously.

To increase clarity and conciseness the distributions of characters and character states discussed below are related to taxa and clades developed in the analysis. Clades are referred to by the names of the taxa (species or genera) on the extreme left (top) and right (bottom) of the clade as depicted on the cladogram (Figs 23 to 34), reading from left (top) to right (bottom).

Identification of apomorphic states

In many cases an apomorphic character state is identified as such by its distinct complexity and very limited distribution and, to avoid pointless repetition in the following discussion, such instances are not examined individually.

The characters are examined under the following headings:

Male genitalia (characters 1–56); Female genitalia (characters 57–97); Reproduction (character 98); Male terminal abdominal segments (characters 99–109); Antennae (characters 110–124); Head (characters 125–128); Legs (characters 129–130); Postcoxale (character 131); Spiracles (characters 133–138); Abdominal setae (characters 139–156); Abdominal pleural projections and modifications (characters 157–161); Abdominal sclerae (characters 132, 162–164).

Male genitalia (characters 1–56)

Most species of Psocodea have symmetric male genitalia and this state is consequently assumed to be plesiomorphic for the superorder. In a few species of Trichodectidae the genitalia are asymmetric, but differences in the form of the asymmetry in different species (Figs 170, 174, 249) suggest that several independent autapomorphies have been developed. In some cases a characteristic asymmetry is limited to a single species and is therefore of no relevance to phyletic analysis, but the asymmetries described in characters 1, 18, 19 and 29 are more widely distributed and are all employed. The distribution of other apomorphies indicates that character 1, the vertical asymmetric deflection of the lateral struts of the basal apodeme ('b.a.l.s.'), has been developed twice, once in *Felicola* (*S.*) *bedfordi* (Fig. 195), and once in the common ancestor of *F. (F.) cynictis* and *F. (F.) setosus* (Fig. 193).

In most Psocodea the basal apodeme is not fused to the parameres, but in a few Trichodectidae this fusion, considered to be apomorphic, has taken place (character 12). In the *Damalinia* (*D.*) *theileri-harrisoni* clade the posterior ends of the b.a.l.s. are broad and fused exteriorly to the parameres (Fig. 75); this fusion (character 12:1) is unlike that found elsewhere in the family

and is believed on that account to be autapomorphic. In the *Trichodectes* (*S.*) *retusus-mustelae* clade, the *T. (S.) fallax-potus* clade, *Neolutridia lutrae* and *Lutridia exilis* the parameres are also fused to the b.a.l.s. (character 12:1'), but there are no features in the fusion pattern to indicate whether the apomorphy is homologous or convergent in the four clades. There are a number of possible sequences of gains and reversals. The fusion may have taken place three or four times with no reversals; once, to be lost at least four times; or twice, to be lost at least twice. The genitalia of *Lutridia* spp. differ from those found in the sister-group (the *Trichodectes-Neolutridia* clade), being more similar to those of *Protelicola*. Comparison of *L. exilis* and *L. matschiei* (Figs 144, 145) indicates fusion of the parameres and b.a.l.s. in the former species to be associated with the virtual detachment of the basal fused portion of the parameres, a unique feature. For this reason the fusion in *L. exilis* is deemed to be autapomorphic. The *Trichodectes* (*S.*) *retusus-mustelae* clade and the *T. (S.) fallax-potus* clade are placed by character 144 in a trichotomy with *T. (S.) emeryi*, a species in which the parameres are not fused to the b.a.l.s. If the fusion is homologous in *Trichodectes* (*Stachiella*) and *Neolutridia*, then it must have been lost in *Werneckodectes*, *Trichodectes* (*Trichodectes*) and *T. (Paratrachodectes)*, and *T. (S.) emeryi*. Parsimony suggests that fusion was developed independently in *Neolutridia* and the common ancestor of the two clades in *Trichodectes* (*Stachiella*) that possess the character, these latter being united as sister-groups. Fusion of the parameres to the b.a.l.s. is thus postulated to have taken place four times in the Trichodectidae, three of those times in the *Trichodectes-Lutridia* clade.

In most Psocodea the parameres are not fused together, but such fusion is present, probably apomorphically, in a number of species of Trichodectidae (character 13:1). In some species parameral fusion is difficult to observe, as the portion of the permanently-everted endophallus lying between the parameres is faintly sclerotised, giving the impression that the parameres are fused together; fusion has probably developed in some cases through sclerotisation of the endophallus. The distribution of other apomorphies suggests that parameral fusion exhibits more homoplasy than any other apomorphy in the analysis, being derived 24 times and lost once. In the *Loriscicola* (*P.*) *bengalensis-juccii* clade the parameres are closely associated with each other but are not fused (Figs 223, 224), although fusion has sometimes been assumed (e.g. Werneck, 1948). This proximity is believed to be autapomorphic for the clade (character 13:1'). The form of the fused parameres (parameral plate) may be apomorphic for groups of species (characters 15, 17).

In a few Trichodectidae the parameres and mesomeres are fused, a probable apomorphy (character 11). The distribution of other apomorphies and slight differences in the fusion pattern (Figs 60, 74, 75, 81, 225) indicate some homoplasy in the character.

As described above, the mesomeres are frequently fused apically in the Psocodea, and consequently this fusion, when found in the Trichodectidae, is deemed to be plesiomorphic. Loss of fusion (i.e. reduction to two unfused mesomeres) is therefore believed to be apomorphic within the Trichodectidae (character 33), and distribution relative to other apomorphies indicates that it has occurred several times in the family (see cladogram). In most species of the *Procaviphilus-Eurytrichodectes* clade there is a lateral desclerotisation on each side of the mesomer arch (Figs 118, 122, 135). This character state is not found elsewhere and this, its structure, and the distribution of other apomorphies, all indicate its apomorphic status (character 34). The mesomer arch may also have lateral flexions (Figs 107, 108, 225), which can give the arch the appearance of being broken (see Werneck, 1948). This modification is found in species of the *Loriscicola* (*P.*) *lenicornis-neoaficanus* clade and of *Procavicola* (*Condylcephalus*), which on the basis of other apomorphies are widely separated on the cladogram; the lateral flexion of the mesomer arch (character 35) is consequently believed to be a convergent apomorphy in the two clades named. In most species of the genus *Eutrichophilus* the mesomer arch is divided into three parts by total desclerotisations laterally (Figs 91, 93). This feature is unique within the Phthiraptera and therefore considered apomorphic (character 36).

In many Trichodectidae a rod-like sclerite terminating posteriorly in a Y-shape or a broad plate is present longitudinally between the b.a.l.s. (Figs 55, 82, 148). Although this sclerite (the

'central sclerotisation') is very clear in some species, it is poorly sclerotised in others, and may be either absent or obscured by the sclerotisations of the endophallus in mounted specimens. The uncertainty attached to the observation of this structure has precluded its use in analysis, although it may be of value taxonomically. The central sclerotisation is probably a derivative of the basal apodeme, developed for muscle attachment.

A sclerite or pair of sclerites is present anteriorly to the parameres in some Trichodectidae, and are referred to here as the 'basiparameral sclerites' (Figs 107, 225) (character 10: 1+2). They may be fused to the parameres (Fig. 225) or to each other (Fig. 93). Their presence is believed to be apomorphic and their derivation is probably from the basal ventral flanges of the parameres found apomorphically (character 28) in a number of Trichodectidae (Figs 118, 122). If they are formed (as suggested here) by detachment of the flange from the main body of the paramere (Fig. 21), fusion of the sclerites and the parameres is a stage in the transformation series to the development of free sclerites, but fusion of the basiparameral sclerites to each other is a 'terminal' apomorphic state (although it is not used in the cladistic analysis because of its extremely limited distribution).

The anterior end of the basal apodeme may be heavily or lightly sclerotised, or apparently not sclerotised at all. This degree of sclerotisation is very susceptible to modification during preparation of the specimen, and thus is difficult to assess accurately. The character is not used in analysis. The most prominent features of the basal apodeme are the lateral struts (b.a.l.s.), which are generally fairly heavily sclerotised. These struts may approach the anterior of the basal apodeme in parallel, convergently or divergently; this character is not used in cladistic analysis because of the difficulty in assigning polarity to the different forms, but is useful taxonomically, and can help in the determination of the form of the anterior margin of the basal apodeme. This anterior margin may be straight or broadly convex, shallowly concave, very deeply concave (Fig. 52) or acuminate (Fig. 173) (character 2). Of these forms the last two are almost certainly apomorphic within the Trichodectidae; the elongation of the apodeme and the concomitant parallel-sided concavity is found only in the *Bovicola alpinus-tibialis* clade (character 2:1), and the acuminate form is found only in three species of *Trichodectes*, although in fact the latter apomorphy imparts little useful information for the construction of the cladogram. The polarity of the character for the other three states is difficult to assess, and they are therefore not used in phyletic analysis.

In some species of *Damalinia* (*Tricholipeurus*) the b.a.l.s. develop a lateral spur before the junction with the parameres, probably at the point at which the dorsal and ventral layers of the basal apodeme separate; this feature (the 'anteposterior spur', Fig. 83) is not found elsewhere in the Trichodectidae and is considered apomorphic (character 5). The posterior ends of the b.a.l.s. are most frequently not, or only slightly, expanded laterally, but in some Trichodectidae they are greatly broadened and scoop-shaped. This very broad form, whilst believed to be apomorphic, is not used as an apomorphy in phyletic analysis because of difficulties in delimiting the state. The posterior forking of the b.a.l.s. (Fig. 173) is also considered apomorphic (character 3), but was probably developed twice in *Trichodectes* (see cladogram). The basal apodeme probably extends anteriorly as far as segment VI in the plesiomorphic state, but in a few Trichodectidae it extends up to segment II; in some cases this lengthening has been accompanied by a width restriction or 'waisting' medially, and this is believed to be apomorphic (character 6). Other features of the basal apodeme are, by virtue of their restricted distribution and concordance with the distributions of other apomorphies, believed to be apomorphic (characters 4, 7, 8, 9).

Whilst it is not possible to be certain of the plesiomorphic form of the parameres in the Trichodectidae, it is assumed that this is fairly unspecialised, and that the forms of the parameres found in groups of species that are also linked by other apomorphies are apomorphic (characters 20-27).

As noted above, apical fusion of the mesomeres is plesiomorphic for the Trichodectidae, so loss of apical fusion, reduction in size and complete loss of the mesomeres are all considered to be apomorphic within the family (characters 30, 31, 33). The presence of a median longitudinal extension to the mesomerarch is also considered plesiomorphic, as it is present in a number of

taxa outside the Trichodectidae. Loss of this extension, or modification of its form from 'simple lanceolate' (Fig. 118), are considered apomorphic within the family (characters 47–49). In the plesiomorphic state the mesomeres articulate basally with the basal apodeme; articulation of the basal apodeme with any other part of the mesomeres is considered apomorphic. Mesad extension of the mesomeres between the b.a.l.s. (character 32) has apparently arisen twice, once in the Dasyonyginae, and once in the *Lorisicola*, and in each case providing an autapomorphy for the clade named. In *Lorisicola* (*P.*) *bengalensis* and *philippinensis* the parts of the mesomeres between the b.a.l.s. are apomorphically deflected posteriad (Fig. 224) (character 37). A similar recurving of the mesomeres occurs elsewhere in the Trichodectidae (character 45), but in this case the mesomeres are exterior to the b.a.l.s., and their recurved portions lie ventrally to the b.a.l.s. This apomorphy is seen as a transformation series of states in *Damalinia* (*Tricholipeurus*) (character 45:1–45:2), the most apomorphic of which (45:2) is also exhibited by *Lorisicola mjoeborgi*, although in this case the recurved parts of the mesomeres are very difficult to see (Fig. 219). Other modifications to the mesomeres believed to be apomorphic are present in restricted groups within the Trichodectidae (characters 38–46).

The endophallus may be sclerotised in a number of apomorphic ways within the Trichodectidae (characters 51–56).

Female genitalia (characters 57–97)

The gonapophyses of most Trichodectidae and many other Psocodea bear at least some setae, which arise directly from the structure and not from tubercles. Absence of setae (character 57) and development of sclerotised setal tubercles (character 58) are therefore both believed to be apomorphic within the Trichodectidae. Setal tubercles are found in *Protelicola*, *Procaviphilus* and the *Trichodectes*–*Neolutridia* clade (*T*–*N*), but as a sister-group relationship between the latter two is not supported by other apomorphies, and the form of the tubercles differs between the two clades (Figs 111, 157), the character is probably convergent. The relationship between *Protelicola* and the *T*–*N* clade is discussed below. The characteristic pattern taken by the tubercles in each clade is modified by loss (character 60) or fusion (character 59); in both cases these are believed to be apomorphic modifications because of their concordance with other apomorphies. Tuberculate setae are also found on the ventral vulval margin of most species in *Trichodectes* (Fig. 157); concordance with other apomorphies suggests the apomorphy of this character (character 74).

The plesiomorphic form of the gonapophyses is not certain, but some forms, because of their very restricted distribution, are believed to be apomorphic (characters 61, 62, 63); some convergence in character 62 is indicated by the distribution of other apomorphies. The development of a lobe on the ventral margin of the gonapophysis is restricted to the Trichodectidae and, for this reason, is believed to be apomorphic within the clade (character 64). Distribution of other apomorphies suggests that the lobe developed independently in several different clades, sometimes taking only one form in a clade (character 70), sometimes being apomorphically modified (characters 66–69). The reduction of the 'spur' – the portion of the gonapophysis distal to the lobe – is considered apomorphic, as it is confined to two small groups of taxa within the family (character 65). Where present, the gonapophyses in most Phthiraptera meet the ventral vulval margin at an angle (Figs 94, 175), but in some Trichodectidae they meet in a smooth curve (Fig. 154), which may be sclerotised (characters 71, 72). The ventral vulval margin may extend in a more or less smooth curve between the gonapophyses, as is most frequently the case in lice with gonapophyses, or it may be produced in some manner (characters 75–78). Each of these projections is considered apomorphic, although the distribution of other apomorphies suggests that some are homoplastically developed in different clades of the family. The distinction between the subgenital lobe (character 78) and the expansion of the ventral vulval margin (character 75, and its apomorphic derivative, character 76), may not be immediately clear, but whilst the former term is applied to structures that arise abruptly from the margin, the latter is a more extensive posterior production of the whole of the margin. Both of these apomorphies occur more than once in the Trichodectidae. The form of the subgenital lobe is variable, though frequently it is marginally serrate, sometimes with the serrations greatly

developed (character 79:2). Several other apomorphies, of restricted distribution within the Trichodectidae, are found in the form of the subgenital lobe (characters 80–83, 85, 86). Two probable apomorphies, the presence of an internal sclerite in the subgenital lobe and the presence of lateral setal patch, are not used in the cladistic analysis. The internal sclerite is not readily observable, but this is probably due to the sclerite being rendered undetectable during preparation of the specimens (especially the smaller species), and this likelihood precludes its use. The distribution of the sclerite, where detected, suggests it to be plesiomorphic within the Trichodectinae, possibly linked to the development of the subgenital lobe in this clade. The lateral marginal setae appear to share part of the distribution of the lateral processes of the lobe (character 81), being absent in a few species only, and the two characters are probably closely associated; for this reason the setal character is not used.

The plesiomorphic form of the genital chamber in the Trichodectidae is not known, but observations on other Phthiraptera suggest light sclerotisation with a few internal spicules. The development, in some restricted groups of Trichodectidae, of particular patterns of spicules, scales, spines and broad sclerotised areas (characters 92–96) is considered apomorphic.

Reproduction (character 98)

Parthenogenetic reproduction (character 98) occurs in a few Trichodectidae, mostly in the Bovicolinae, but also in the species *Geomydoecus scleritus*. As all other Phthiraptera reproduce bisexually, the character is taken as apomorphic. Parthenogenesis appears to have developed at least four times in the Trichodectidae.

Male terminal abdominal segments (characters 99–109)

The sclerites of the terminal segments of the male trichodectid abdomen are very variable in presence or absence states, extent, and degree of subdivision. This variability is not, in many cases, readily associated with transformation series of other characters to which polarity has been applied, and the plesiomorphic state (and hence apomorphic states) of the characters of these sclerites is, in most cases, not known. In a few instances the sclerites are distinctly modified in a restricted group of species, and thus polarity can be assigned (characters 99, 101, 106, 107, 108, 109).

Segment IX and the genital opening are apomorphically positioned more or less dorsally in many species of Trichodectidae, as discussed above. Distortion due to preparative processes obscures the position in many of the specimens examined, however, and characters associated with this positioning cannot be used with any confidence, and are excluded from analysis.

In some species of Trichodectidae the posterior margin of tergum IX is greatly expanded to produce a double convex lobe (character 100); this development is believed to be apomorphic, although the distribution of other apomorphies indicates that it developed twice.

The presence of pseudostyli, discussed in detail above, is believed to be apomorphic for the Trichodectidae (character 102). The plesiomorphic form of the pseudostyli is not known, as the extant forms are very variable and cannot, in most cases, be resolved into transformation series. In two cases (characters 103, 104), the pseudostyli are of very distinct form and restricted to groups of species believed to be holophyletic on other grounds; these character states are believed to be apomorphic. The presence of a single projection posteriorly on segment IX in some species of Trichodectidae, believed to be formed of fused pseudostyli, is also considered apomorphic (character 105). Although found in only three species, the distribution of other apomorphies suggests two independent developments of this character state.

Antennae (characters 110–124)

In all Trichodectidae the male flagellomeres are fused together (character 111), a state found elsewhere only in the anopluran families Echinophthiriidae and Hamophthiriidae and therefore considered apomorphic for the Trichodectidae. Fusion of the flagellomeres has also occurred in some female Trichodectidae (character 110), but the distribution of other apomorphies suggests four homoplastic derivations of this apomorphy in the family. The expansion of the scape in the male to house the enlarged musculature is probably plesiomorphic for the Trichodectidae, as

similar expansion is found in many Ischnocera and Anoplura. Reduction of this expansion is, however, apomorphic within the family (character 112), and is believed to have taken place three times. The flagellum of most male Trichodectidae bears a number of setae modified into broad pointed 'teeth' (Figs 13, 231), a feature not found in the same form in any other Phthiraptera, and therefore considered apomorphic for the family. The plesiomorphic number of 'teeth' is almost certainly two, as this number is the most common in all groups of Trichodectidae; any variation from this number (to zero, one, three, four or eight) is believed, therefore, to be apomorphic (character 115). The loss of the basal articulation of the 'teeth' (character 117) and the development of a supporting protuberance (character 116) are both apomorphic. In order that the male antennae should clasp the female with maximum efficiency the 'inner' (posterior) surface of some or all of the antennal segments may be roughened or bear projections; such developments are considered apomorphic in each form (characters 118–121). The presence of a membranous projection on the female antenna (character 122) is also believed to be apomorphic. In most Phthiraptera the setae of the scape are scattered over its surface in no coherent pattern, and this is true of some Trichodectidae (Fig. 70); in most Trichodectidae, however, the setae of the dorsoposterior surface of the scape are apomorphically arranged in a line along the segment (Fig. 13) (character 113). In some cases where a row of setae might be expected from the construction of the cladogram, the number of the setae involved in the putative row is only two, and this is believed to represent an apomorphic reduction in number (character 118).

The sensilla of the antennae in Trichodectidae and other Phthiraptera have been discussed above; the presence of a fringed pit surrounding the sensilla of the flagellum in two species of Trichodectidae is unique and believed to be apomorphic (character 124).

Head (characters 125–128)

Although the sitophore sclerite is variable in most Phthiraptera (Haub, 1973), it is comparatively uniform in the Trichodectidae. The form found in most Trichodectidae (Fig. 11) is believed on this account to be plesiomorphic, and is departed from in *Bovicola* (*Spinibovicola*), *Dasyonyx* and *Eurytrichodectes*, where the posterior arms are extended (Fig. 12) (character 125). The distribution of other apomorphies indicates that the modification is convergent in *Bovicola* (*Spinibovicola*) and *Dasyonyx* plus *Eurytrichodectes*.

The posterior margins of the temple are generally broadly rounded in Trichodectidae, but in species of the genus *Eutrichophilus* the convexity is much greater than in the rest of the family (Fig. 87); this development is believed to be apomorphic (character 127). In the three species of the genus *Eurytrichodectes* (only two of which are described) and the four of *Procavicola* (*Condylcephalus*) the posterior temple angles are developed into pointed projections (character 126), these being very long in the former genus (character 126: 2). This modification is not found elsewhere in the Trichodectidae, although small rounded projections are found in some *Dasyonyx* spp. and some *Damalinia* spp. The presence of pointed projections is believed, on the basis of the distribution of other characters, to be homoplastic in the two genera mentioned.

The form of the osculum has been largely excluded from consideration in the cladistic analysis because of the direct influence of the hair of the host (see above). However, in the *Damalinia* (*D.*) *theileri-baxi* clade it is quite different from other species of Trichodectidae (Fig. 69), and is here suggested to be apomorphic (character 128).

Legs (characters 129, 130)

The loss of one tarsal claw on each leg (character 129) is an apomorphy associated with ectoparasitism on mammals. This character is proposed as an autapomorphy of the Trichodectidae, although it may be autapomorphic for a postulated holophyletic group comprising the Anoplura, Rhyncophthirina and Trichodectidae (Lyal, 1985).

A number of Psocodea have teeth on the 'inside' face of the tarsal claws, and many Trichodectidae have what appears to be a single basal tooth (Fig. 15). The occurrence of teeth all along the 'inside' face of the tarsal claws (Figs 14, 15) is restricted in the Trichodectidae to *Dasyonyx*, and is believed to be autapomorphic for the genus (character 130). The two

subgenera of *Dasyonyx* have tarsal claw teeth of different forms: *D. (Dasyonyx)* have sharp slender teeth (Fig. 14), whilst *D. (Neodasyonyx)* have blunter, broader teeth (Fig. 15). These two forms may be co-apomorphies, indicating that the subgenera are sister-groups, or one may be the plesiomorphic state. No other characters have been found within *Dasyonyx* that indicate reliable sister-group relationships within the genus. In this study the two tooth forms are accepted as co-apomorphies and the subgenera retained, but further work on the genus may cause this hypothesis to be challenged.

Postcoxale (character 131)

In most species of Trichodectidae the metathoracic postcoxale is either not sclerotised or sclerotised and small, but the polarity of the transformation series with the extreme states 'sclerotised' and 'not sclerotised' is not known. In *Procaviphilus (Meganarionoides)* and some species of *Dasyonyx (Dasyonyx)* the postcoxale is greatly enlarged and heavily sclerotised, an apomorphic state not included in the analysis for reasons given below. A further apomorphic condition, the fusion of the postcoxae, is also found in some members of the same subgenera. The presence of the sclerotised postcoxale is difficult to determine in some of the smaller species of *Dasyonyx*, but in any case the distribution of other apomorphies indicates convergence of the postcoxale characters in the two subgenera. Neither apomorphy is used in the analysis.

In *P. (Meganarionoides)*, uniquely, the postcoxale is fused to abdominal pleurum II (character 131), and this apomorphy is used in the analysis.

It is interesting that the great development of the postcoxae, restricted to lice parasitic on hyraxes, is morphologically convergent on the development of the apophysis of abdominal sternum II (character 132), which is found in another group of hyrax lice.

Spiracles (characters 133–138)

For the Phthiraptera (and the Trichodectidae) the plesiomorphic number of spiracles is a single thoracic pair and six abdominal pairs; further reduction in the number of abdominal spiracles is apomorphic. The numbers of abdominal spiracles in the different species of Trichodectidae are summarised in Table 1. Each reduction is considered to be an apomorphy (characters 135–138), though some homoplasy has occurred. Inspection of the distribution of other apomorphies indicates that reduction to five, four and one pair of spiracles has occurred once, reduction to three and two pairs twice, and reduction to none eight times. Because of the sequential pattern of spiracle loss, apomorphy 136 is always associated on the cladogram with apomorphy 135, 137 with 136 and 135, and 138 with 137, 136 and 135.

In most species of lice all of the abdominal spiracles have atria of roughly the same size; as has been pointed out in earlier discussion, however, some Trichodectidae have posterior spiracles with atria much smaller than those more anterior on the abdomen (character 134). This difference in size is believed to be an apomorphic reduction.

In most species of lice the atrium of the thoracic spiracle is as broad or broader than long; species of the genus *Cebidicola*, however, have a tubular atrium associated with the thoracic spiracle (character 133). This modification of form is believed to be apomorphic.

Abdominal setae (characters 140–156)

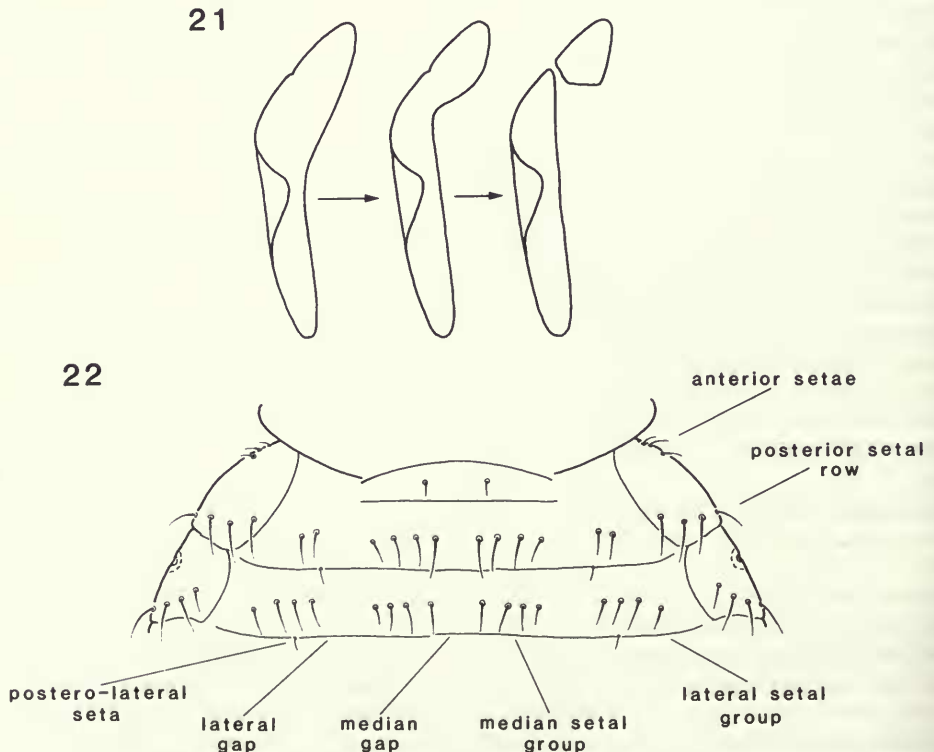
Study of abdominal setal patterns throughout the Psocodea suggests that the plesiomorphic pattern is a row of setae running around the abdomen on each of segments I to VIII. On trichodectid abdominal pleura II–VII this row of setae (referred to here as the posterior setal row or 'p.s.r.') is generally clear, and is absent in only a few species. The distribution of other apomorphies indicates this absence to be apomorphic, although limited to a very few, distantly-related, species. In some Trichodectidae, the p.s.r. of pleura II, III and IV comprises setae that are much stouter than those of other pleura, and the distribution of other apomorphies suggests the apomorphic status of each of these, although each exhibits some homoplasy. Preliminary analysis indicated that specialisation of the p.s.r. on pleura II and IV conveys little phylogenetic information, and only character 139 (specialisation of the p.s.r. on pleurum III) is used in the final cladistic analysis. The setae on pleura VIII and IX are frequently longer than the setae of

the p.s.r. on anterior pleura; the extreme length of these setae in *Eutrichophilus* is, however, recognised as apomorphic (character 140).

The setal row on sterna II and III is usually similar to the row on other sterna, but in the two species of *Eurytrichodectes* the setae of these two rows are short, stout and conical (Fig. 136). This unique feature is believed to be apomorphic (character 153).

The tergal setal row of many Trichodectidae, especially males, is clearly composed of four discrete groups – two lateral and two median – each separated by a gap (Fig. 22). The positioning of the groups and the number of setae in them are useful taxonomic characters, and may be utilised as landmarks for the identification of particular setae. The groups are, however, difficult to use in phyletic analysis because of the difficulty of assigning polarity to any transformation series.

In some Trichodectidae (and in no other Phthiraptera) a seta – termed here the ‘posterolateral seta’ or ‘p.l.s.’ – is present posterolaterally on each side of terga II–VI (Fig. 22). The restriction of distribution of this seta within the Phthiraptera suggests that its presence is apomorphic (character 151). In some cases there is more than one p.l.s. on each side of the tergum (Fig. 201); this is believed to be an apomorphy but its sporadic occurrence (in terms of clades indicated by other apomorphies) has led to its omission from the cladistic analysis. The presence of the p.l.s. is difficult to assess in some species, either because the lateral group may be reduced in number or because the lateral group is composed of very long setae. In the former case, a single seta in the position of the p.l.s. may be this seta (the lateral group being absent), or it may be the sole remaining seta of the lateral group (the p.l.s. being absent) (Fig. 159). In the latter case (most *Trichodectes* species and the Neotrichodectinae), the most lateral seta of the lateral group frequently lies slightly posterior to the rest of the row (Fig. 158) and a more differentiated p.l.s. is absent. In both these cases the p.l.s. is postulated to be present, though modified. The



Figs 21, 22 Trichodectid morphology. 21, postulated evolution of basi-parameral sclerite by detachment of basal flange of paramere. 22, Abdominal setal arrangement, illustrated by anterior terga and pleura of male.

distribution of other characters suggests, however, that secondary loss of the p.l.s. has occurred within some taxa.

Some setae of the median tergal group, particularly in males, may be specialised. In males of *Neotrichodectes* spp. the two central setae of the united median groups, or two setae very near the centre (perhaps separated by one or two unmodified setae) are very much smaller than the other setae of the row (Fig. 229). These 'tergocentral microsetae' (character 152) are found nowhere else, and this and the concordance of their distribution with that of apomorphy 118: 1'+2' suggests the apomorphy of the character state. In *Felicola* (*S.*) *pygidialis* and *F.* (*S.*) *macrurus* the median group of tergum III is modified in a distinctive manner in the males (Fig. 178), and this modification is assumed to be apomorphic for the two species (character 147). Some or all of the setae of the median group on terga II and III of male Trichodectidae may be enlarged relative to the other tergal setae. This enlargement occurs sporadically both within and outside the family, and each case is believed to be autapomorphic. Within the Trichodectidae, in males of *Geomydoecus* (*Thomomydoecus*), *G.* (*G.*) *copei*, *Trichodectes* (*Paratrichodectes*) *ovalis* and *ugandensis*, and the undescribed sister-subspecies of *Trichodectes* (*T.*) *galictidis*, the setae of the median row on both terga II and III are enlarged but remain in a straight row (Figs 161, 244); this arrangement is believed to be apomorphic, but probably convergent in each of the four groups (character 149). In *Bovicola* (*Spinibovicola*) *hemitrangi* and *multispinosa* a similar enlargement is confined to some of the setae of tergum II, and the lines are curved (Fig. 41) (character 150). In males of *Felicola*, the holophyly of which is supported by several apomorphies, the median setal group is reduced to a single, greatly enlarged seta (Fig. 188). The apomorphic status of this character (character 142) is indicated by its restricted distribution and correlation with other apomorphies. It is notable that the setae are single, but of normal size (very small) in the *Felicola* (*F.*) *rahmi-viverriculae* clade (Fig. 183), and secondarily increased in number to six in *Felicola* (*S.*) *bedfordi* and *F.* (*F.*) *setosus* (Figs 180, 189). On the basis of other apomorphies, the former is believed to be a single autapomorphic reversal, whilst the latter is believed to be a convergent gain.

The sclerite from which the pair of setae arises may be long and of characteristic shape (Fig. 181); this feature is found only in conjunction with the enlarged setae (character 142) and is postulated to be apomorphic (character 155).

In many males of *Felicola* the median setal group on terga III–VII is also reduced to a single seta, although in most cases this does not approach the size of the seta of tergum II. In the *Felicola* (*S.*) *cooley-quadriceps* clade this reduction has taken place on terga III–VII, but the setae are similar in length to those of tergum II, the latter being reduced relative to those of other species of *Felicola* and the former enlarged (Fig. 186) (character 143). This apomorphy is convergent on the apomorphic setal pattern of the males of *Trichodectes* (*Stachiella*) (character 144), although in this case the setae are all generally long and stout. The median setal group of the female tergum may also be reduced to a single seta (character 145) or lost (character 146). The distribution of these female apomorphies is as follows. The reduction of the median group to a single seta is found only in the *Trichodectes* (*S.*) *fallax-octomaculatus* clade; the sister-species, *T.* (*S.*) *potus*, and the sister-group to this clade, the *T.* (*S.*) *retusus-mustelae* clade, lack the female median group entirely. The sister-species to the whole *T.* (*S.*) *retusus-potus* clade, *T.* (*S.*) *emeryi*, has the median group unreduced, numbering three setae, on terga I and II, reduced to one seta or absent on tergum III, and absent on terga IV–VIII. It is not certain whether setal loss in the female has taken place only once, the setae being regained in the *fallax-octomaculatus* clade, or has taken place independently three times (in *emeryi*, the *retusus-mustelae* clade, and *potus*).

The length of the abdominal setae is difficult to employ in phyletic analysis because of the problem of establishing the polarity of the transformation series 'very short – medium – very long'. The restricted distributions of the two extremes of the series (concordance with other apomorphies) indicate their apomorphic status, however. The very short, sparse setae (Fig. 183) are found in no other Phthiraptera but the *Felicola-Loricicola* clade and some *Trichodectes* spp., and are probably apomorphic but convergent in the two groups. The very long refringent setae of some Trichodectidae (Fig. 158) are considered apomorphic for a similar reason (character

141), though in this case similar setae are found in some Philopteridae. These long setae probably evolved twice in the Trichodectidae: once in *Trichodectes* and once in the Neotrichodectinae. The fine, long setae of the females of the *Felicola* (*S.*) *cooleyi-quadraticeps* clade are found in no other group and are considered apomorphic (character 154).

The setal bases – the circular ‘pits’ of the setal articulations – are of fairly constant size relative to the setae in most Trichodectidae. However, in the *Bovicola* (*B.*) *alpinus-tibialis* clade the bases are noticeably large in relation to the setae, and seem to have a double margin. This feature needs to be examined using the scanning electron microscope to elucidate its true structure, but examination using the light microscope is sufficient to detect its presence. This feature is here considered as apomorphic (character 156).

Abdominal pleural projections and modifications (characters 157–161)

In many Trichodectidae the dorsoposterior and/or the ventroposterior pleural angles project on pleura II, III or IV (see discussion above, and Table 2). Projections on these segments of the type found here do not occur elsewhere in the Phthiraptera, and are therefore considered as apomorphic (characters 158–160). Preliminary analysis reveals that the projections on pleurum III contribute no useful phyletic information, so the apomorphy is omitted from the final cladistic analysis. Variation in the degree of development of the dorsal and ventral lobes of the projection on pleurum IV is omitted for the same reason, except for the extreme development in *Eurytrichodectes* (character 161). Both the presence of a dorsal and a ventral projection on pleurum IV (characters 159 and 160 respectively) are included in the analysis, though the latter apomorphy is reversed in some clades. The presence of a projection on pleurum II (character 158) provides a synapomorphy for *Geomydoecus* spp., which are also united as a holophyletic group on other grounds; the projection on this pleurum is found convergently in *Trichodectes* (*Paratrachodectes*) *zorillae*. The sclerotisation of the dorsal projection on pleurum II (character 158:2) is an autapomorphy of *Geomydoecus* (*Thomomydoecus*) (and some species in *Geomydoecus* s.str. – see discussion below –) and *T. zorillae*, but sclerotisation of the projections on the other pleura is very variable, and is not used in cladistic analysis.

In *Damalinea* (*Damalinea*) pleurum II extends on to sternum II, and the pleurite is expanded at the expense of the sternite (character 157). This extension may be broad (character 157:1') or narrow (character 157:1), but the more plesiomorphic state of these two (should they not be co-apomorphies) is not known. The species with a broad ventral extension of pleurite II also possess a more or less extensive dorsal extension, but this is not found in species with a narrow ventral extension. In this treatment the two forms of the ventral extension are used to characterise each of two sister-groups, but this hypothesis is open to challenge, as the group indicated by character 157:1 has no other supporting apomorphy.

Abdominal sclerae (characters 132, 162–164)

As noted above, in species of the trichodectid genus *Procavicola* sternite II is greatly developed as a heavily sclerotised internal apophysis, articulated to pleurum II (character 132). The presence of this unique structure is considered apomorphic.

The presence of the lateral flecks and their associated small sclerite is considered apomorphic, as the structure occurs in no Phthiraptera other than the Trichodectidae (character 164).

The pleura, sterna and terga of the trichodectid abdomen may be sclerotised or not; although some groups (identified on the basis of other apomorphies) may, in general, be more or less sclerotised, the polarity of the transformation series ‘sclerotised – not sclerotised’ for each segment cannot be determined, and these characters are not used in the cladistic analysis. The male abdomen may have a characteristic sclerotisation dorsally, in that the terga may have anterior and posterior sclerites; this feature is present in some Anoplura, but is probably convergent in this suborder. The presence of doubled tergal sclerites in male Trichodectidae is believed to be apomorphic for the family, but is not used in cladistic analysis because of the large number of reversals. The tergal sclerites are not further modified in most male Trichodectidae, but in some there is longitudinal division of the anterior or posterior sclerites (characters 162 and 163 respectively), this division being accepted as apomorphic.

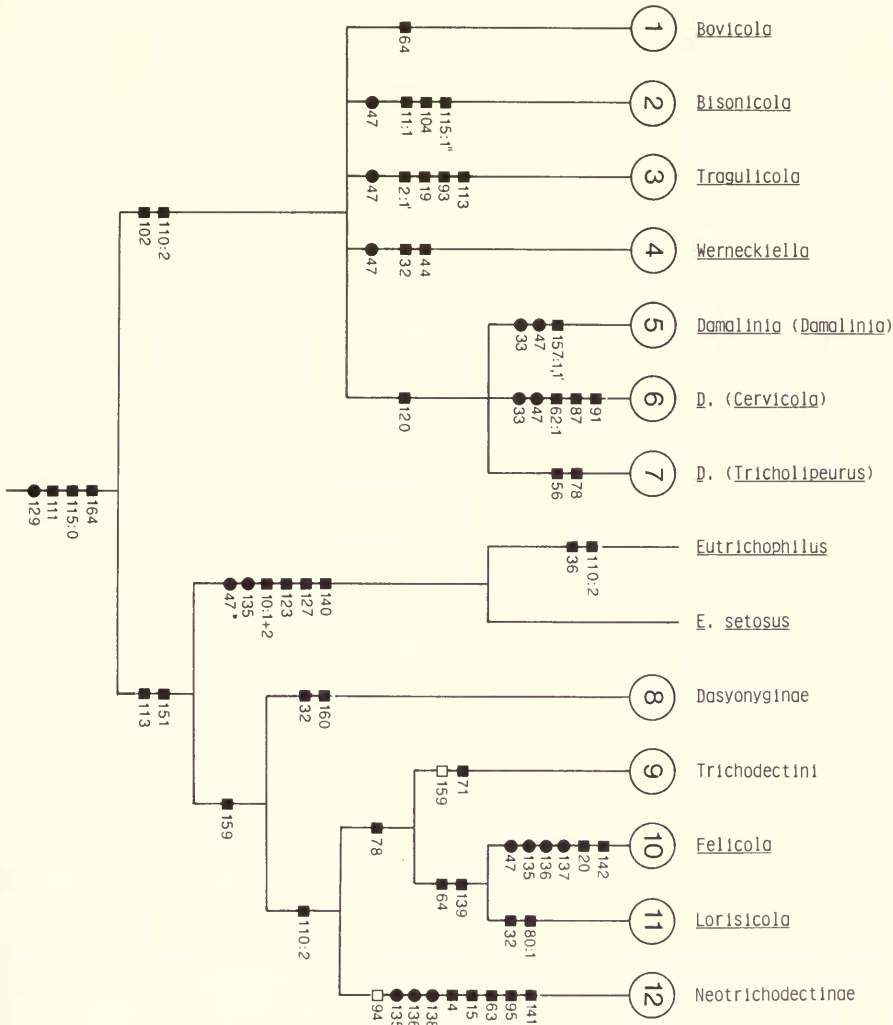


Fig. 23 Cladogram of Trichodectidae. Clades numbered 1–12 are resolved in Figs 24–34. The Eutrichophilinae (Genus *Eutrichophilus* only) is not resolved further. For explanation of numbered apomorphies see text.

Cladistic analysis

The holophyly of both monotypic and polytypic species is accepted without the need for justification, so species-level autapomorphies have not been indicated unless they are homoplastic with character states elsewhere on the cladogram. Omission of the autapomorphies of species saves both space in the data matrix and time taken for analysis, and for the same reasons many sister-species pairs are justified on the cladogram with fewer autapomorphies than are available.

Of the 187 apomorphic character states used in the analysis, 86 are postulated to have been developed more than once or to have been secondarily lost, 363 such homoplasies being proposed. When, in the analysis, a choice is available between postulating one reversal or a pair of homoplastic gains (i.e. three clades in a holophyletic group are involved and the topography of the tree is not affected whichever the choice), the latter is chosen (e.g. character 13:1 in the *Damalinia theileri*–*appendiculata* clade). This choice is made so that the distribution of apomorphic character states can more easily be discerned on the cladogram. The number of

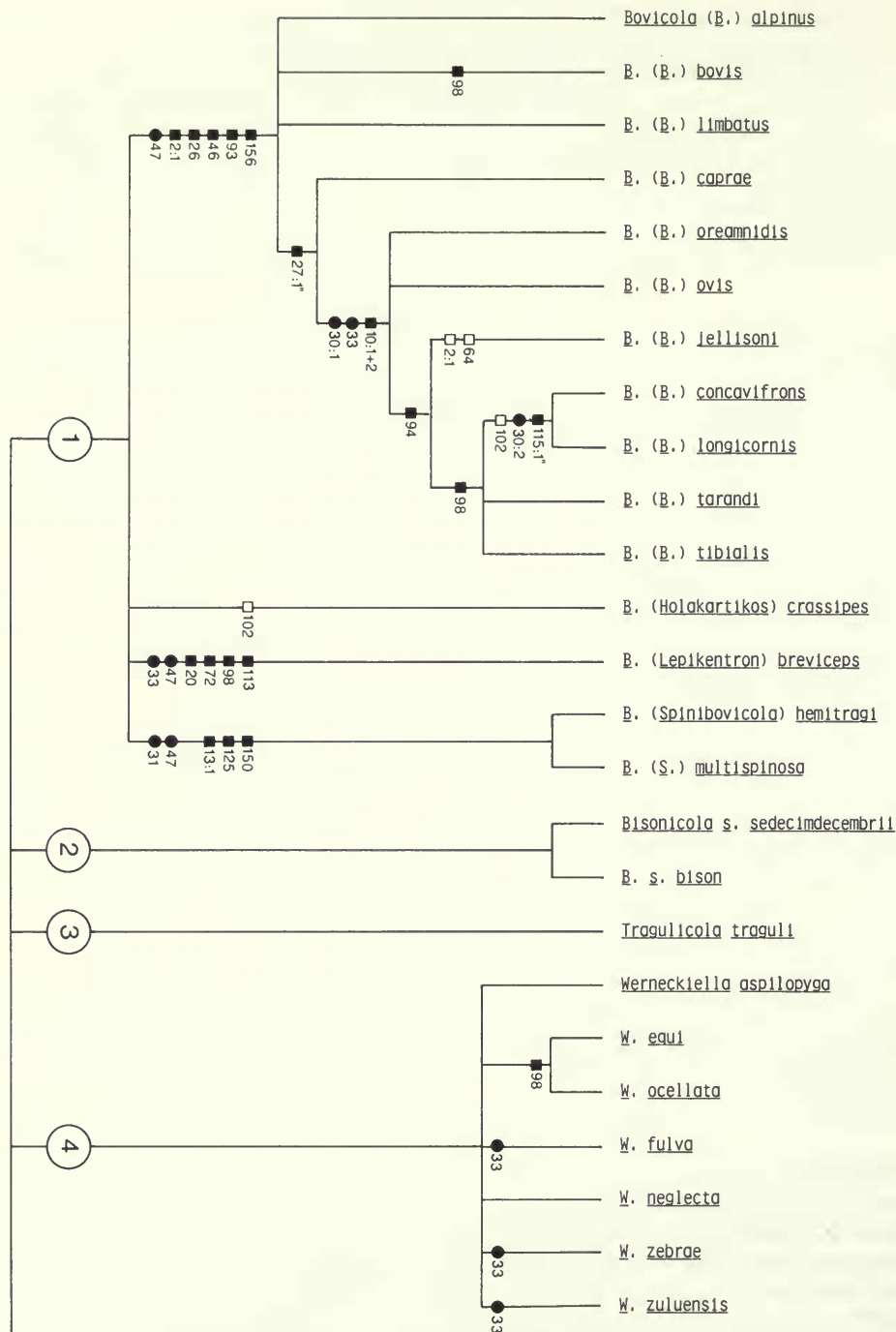


Fig. 24 Cladogram of Bovicolinae (part) (clades 1-4 of Fig. 23: genera *Bovicola*, *Bisonicola*, *Tragulicola* and *Werneckiella*). For explanation of numbered apomorphies see text.

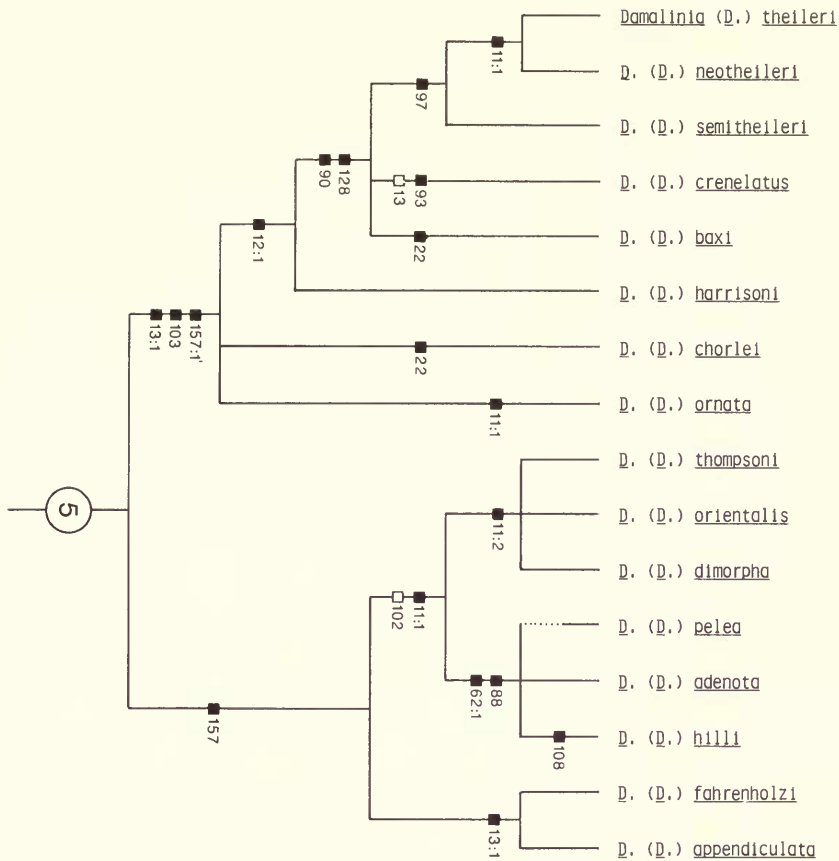


Fig. 25 Cladogram of *Damalinia* (*Damalinia*) (clade 5 of Fig. 23). For explanation of numbered apomorphies see text.

homoplasies could be slightly reduced without affecting the topology of the tree because, as explained below, the less parsimonious presentation is sometimes chosen to make the cladogram more informative and less potentially misleading. In a number of places in the discussion of apomorphic state identification above, reference is made to single apomorphic character states arising more than once. This is superficially contradictory, especially if the terms apomorphy and homology are equated. Such situations have been detected during one 'round' of reciprocal illumination. Should all such convergent apomorphic states be recoded as separate apomorphies (which they are believed to be, even if they cannot be differentiated morphologically) the cladogram would appear more parsimonious.

The loss of the median extension of the mesomerar arch (character 47) is placed on the cladogram 17 times, frequently in combination with the loss of apical fusion of the mesomeres (character 33). These apomorphies are not arranged in the most parsimonious manner on the cladogram, as can be seen by inspection of the Bovicolinae. As presented, the cladogram depicts the loss of the extension 11 times in this subfamily. A more parsimonious arrangement of the apomorphies is achieved by postulating characters 33 and 47 as synapomorphic for *Damalinia* (*Damalinia*) and *Damalinia* (*Cervicola*), and character 47 as synapomorphic for two clades: *Werneckiella* plus *Tragulicola* and *Bisonicola*, and *Bovicola* (*Bovicola*) plus *B. (Lepikentron)* and *B. (Spinibovicola)*. This arrangement reduces the number of proposed homoplasies of character 47 to six within the Bovicolinae, and reduces the number of polychotomies on the cladogram. Alternatively, the loss of the extension might be postulated to have occurred only once, in the common ancestor of the Bovicolinae, and regained six times (*B. crassipes*, *D.*

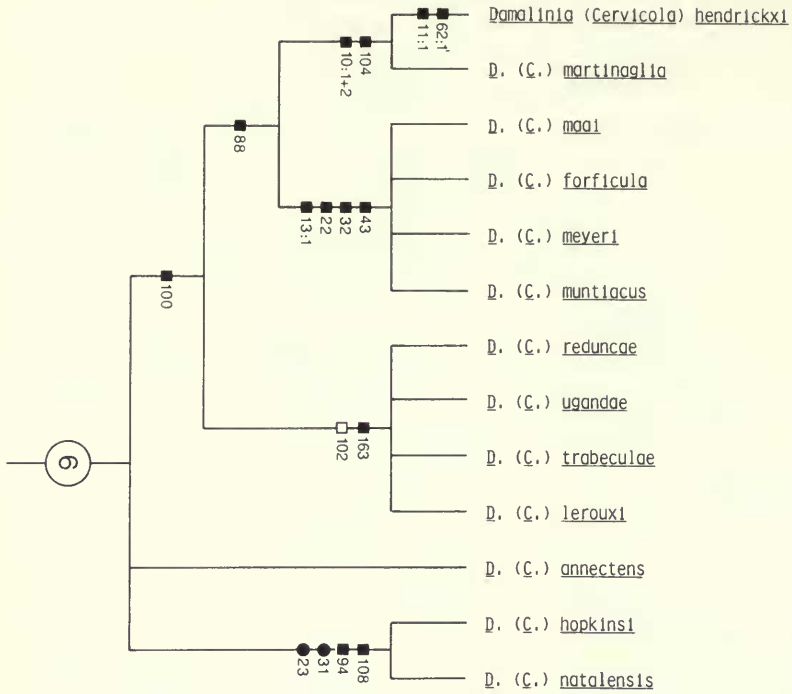


Fig. 26 Cladogram of *Damalinia (Cervicola)* (clade 6 of Fig. 23). For explanation of numbered apomorphies see text.

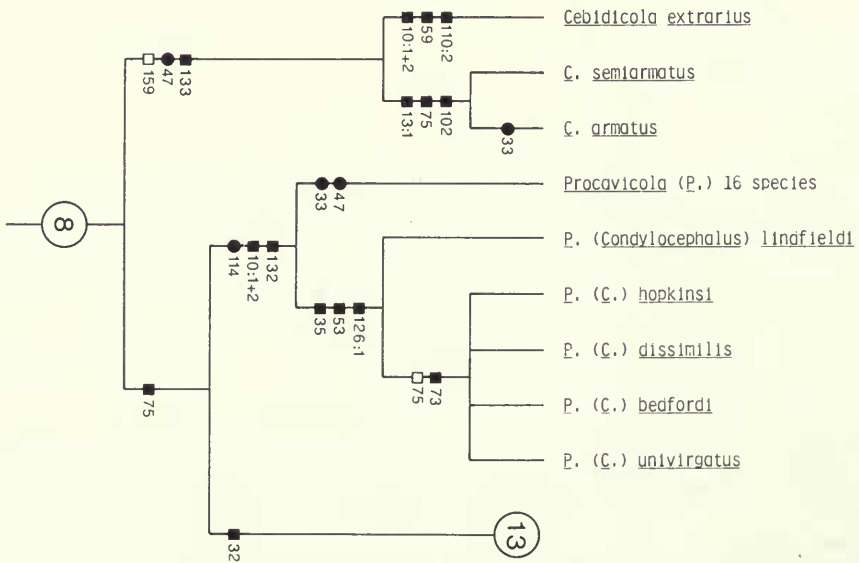
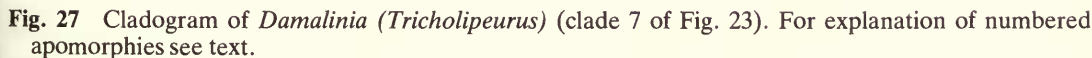
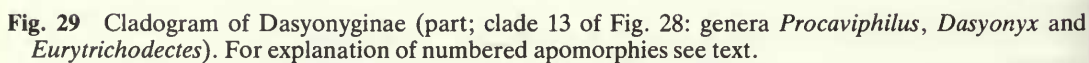


Fig. 28 Cladogram of Dasyonyginae (clade 8 of Fig. 23, part: genera *Cebidicola* and *Procavicola*). Clade 13 is resolved in Fig. 29. For explanation of numbered apomorphies see text.



elongata, *D. moschatus*, *D. clayi* and the *D. albimarginata-indica* clade). The most parsimonious hypothesis is that the structure was lost in the ancestor of Bovicolinae as suggested above, regained twice (*B. crassipes* and the *D. (T.) albimarginata-elongata* clade), and secondarily lost twice (*D. (T.) lineata-victoriae* and *D. (T.) pakenhami-bedfordi*). This last hypothesis, although more parsimonious than the distribution on the tree presented, does not change the topology of the tree. The distribution of character 47 is not as apparent from inspection of the tree in its most parsimonious distribution as it is in the tree presented, as the more scattered distribution of the losses and reversals obscures the alternative possible distributions and implies a spurious confidence in the tree as supported by them.

The distribution of character 33 (the loss of mesomeral fusion) in *Werneckiella* is not presented in the most parsimonious manner. There is great difficulty in the observation of this character state in *Werneckiella*, and the morphological difference between 'loss of fusion' and 'fusion' is very slight. A detailed examination of the species of this genus for other characters to



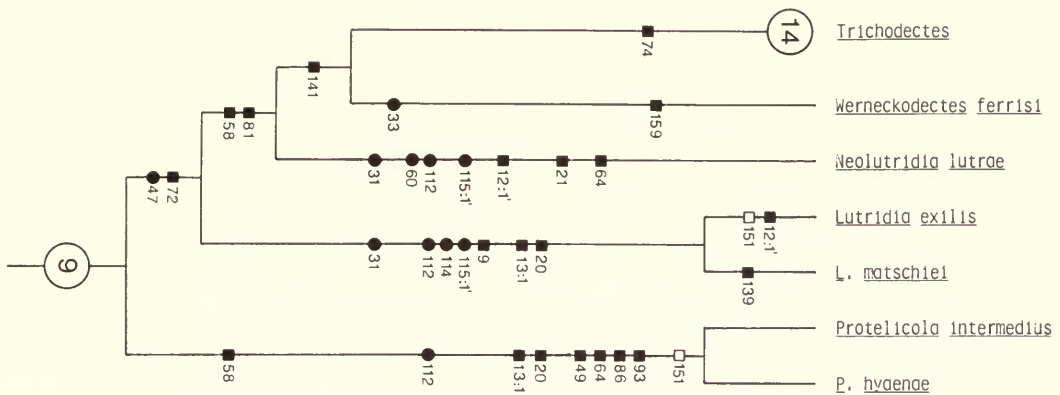


Fig. 30 Cladogram of Trichodectini (clade 9 of Fig. 23, part: genera *Protelicola*, *Lutridia*, *Neolutridia* and *Werneckodectes*). Clade 14 is resolved in Fig. 31. For explanation of numbered apomorphies see text.

complete a full analysis was not made, character 33 only being noted because it occurs elsewhere on the cladogram. It is possible but not likely that the distribution of character 33 as observed is supported by other apomorphies, but the proposal of holophyletic groups within the genus on the basis of the observations made of this single character would be unwise. It is notable that *Werneckiella fulva* and *W. neglecta*, which differ in the state of character 33, are otherwise very similar, the females apparently being indistinguishable (Emerson & Price, 1979), and it is very likely that they are sister-species.

The arrangement of *Protelicola*, *Lutridia* and the *Trichodectes*–*Neolutridia* clade (*T*–*N*) on the cladogram (Figs 30, 31) does not accord with the most parsimonious distribution of the apomorphies. The cladogram contains four convergences for 'gain' apomorphies: 12:1' (fusion of parameres and b.a.l.s.) is postulated as homoplastic in *Lutridia*, *Neolutridia* and *Trichodectes* (*Stachiella*); 13:1 (fusion of parameres to each other) is postulated as homoplastic in *Protelicola* and *Lutridia*; 20 (development of rod-shaped parameres) is postulated as homoplastic in *Protelicola* and *Lutridia*; and 58 (development of tubercles for the gonapophysis setae) is postulated as homoplastic in *Protelicola* and *T*–*N*. Apomorphy 12:1' has been discussed in detail above, and the distribution suggested in the cladogram is believed consistent with the morphological evidence. Apomorphy 58 could be considered in two ways other than that presented: as an autapomorphy supporting the sister-group relationship of *Protelicola* and *T*–*N*, or as an autapomorphy of the Trichodectini (the *Trichodectes*–*Protelicola* clade), reversed in *Lutridia*. The first alternative is not supported by the distribution of any other apomorphies, whereas the two alternative arrangements are each indicated by more than one apomorphy (see below); the sister-group relationship of *Protelicola* and *T*–*N* is therefore rejected. The plesiomorphic arrangement of the gonapophysis tubercles in *T*–*N* is clearly distinct from the arrangement in *Protelicola*. If the tubercles are postulated to be homologous in the two clades two further apomorphies (the form of the tubercles in each clade) would have to be proposed, as neither form appears to be plesiomorphic with respect to the other. This manipulation does not affect the topology of the cladogram (whatever the position of *Lutridia*), and does not clarify the relationships of the clades involved, so the hypothesis of convergence of character 58 in *Protelicola* and *T*–*N* is retained. The other two apomorphies may now be considered together as they both suggest the sister-group relationship of *Protelicola* and *Lutridia*. The alternative hypothesis (of the cladogram as presented) is supported by apomorphies 72 (development of a sclerotisation along the ventral vulval margin) and 47 (loss of the median extension of the mesomer arch). 'Loss' characters are given much less weight than 'gain' characters in this analysis, so character 47 should be left out of consideration. The sister-group relationship of *Protelicola* and *Lutridia* is therefore supported by two apomorphies and the relationship proposed on the cladogram supported by one. As noted in the generic descriptions below, however, an undescribed species of *Protelicola* has been seen which does not share apomorphy 20. The cladistic position of this species with respect to the other two species in the genus has not

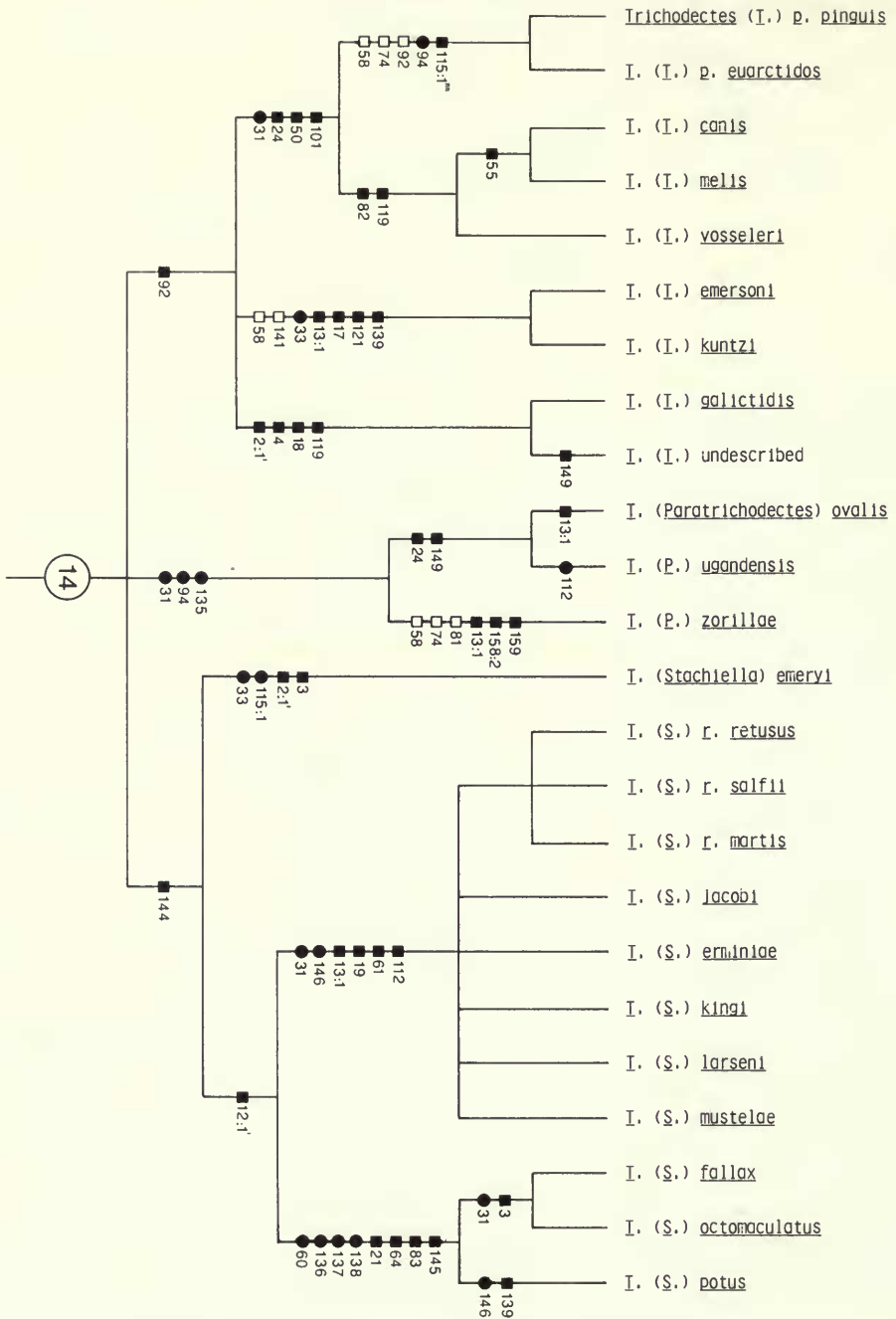


Fig. 31 Cladogram of *Trichodectes* (clade 14 of Fig. 30). For explanation of numbered apomorphies see text.

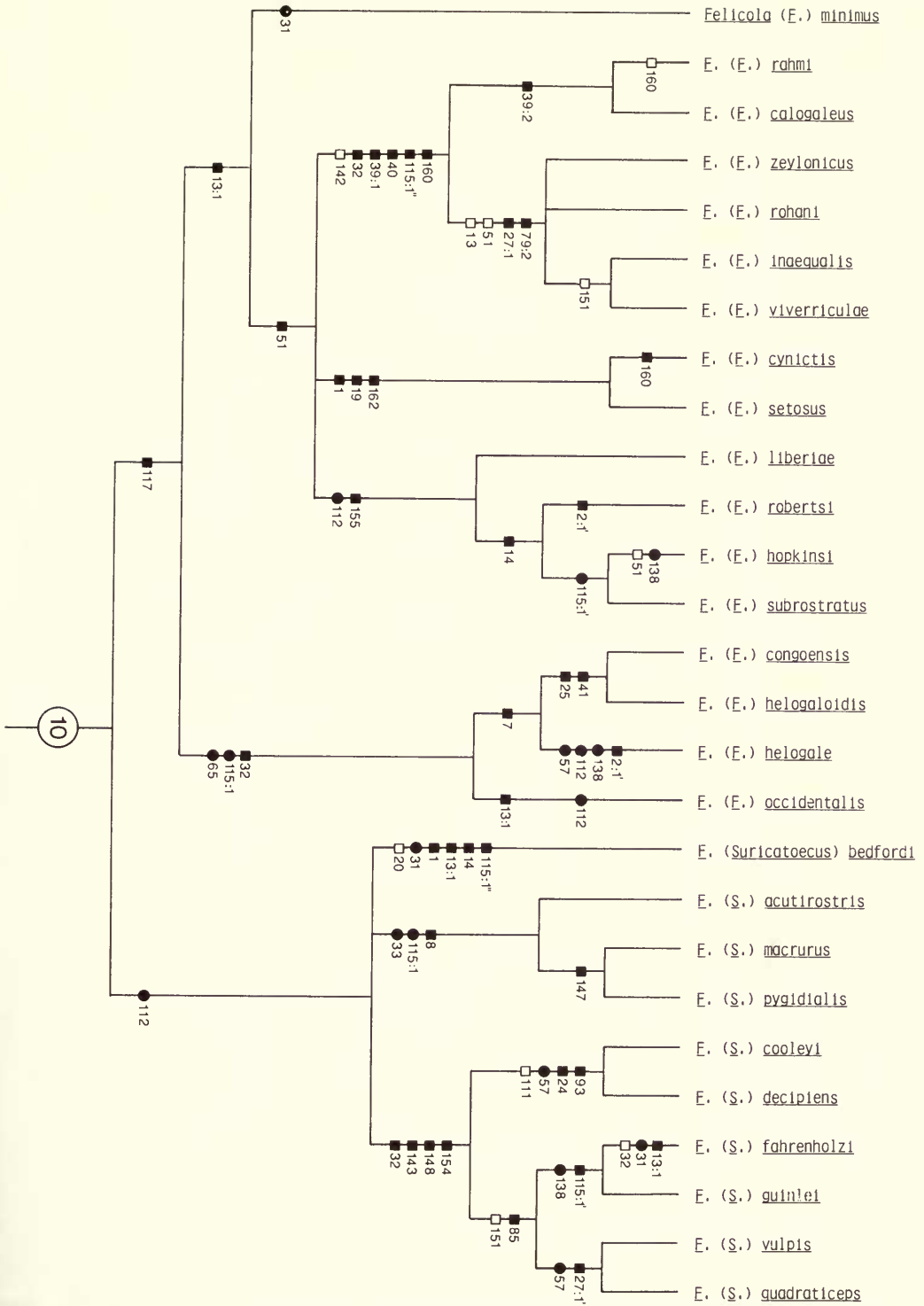


Fig. 32 Cladogram of *Felicola* (clade 10 of Fig. 23). For explanation of numbered apomorphies see text.

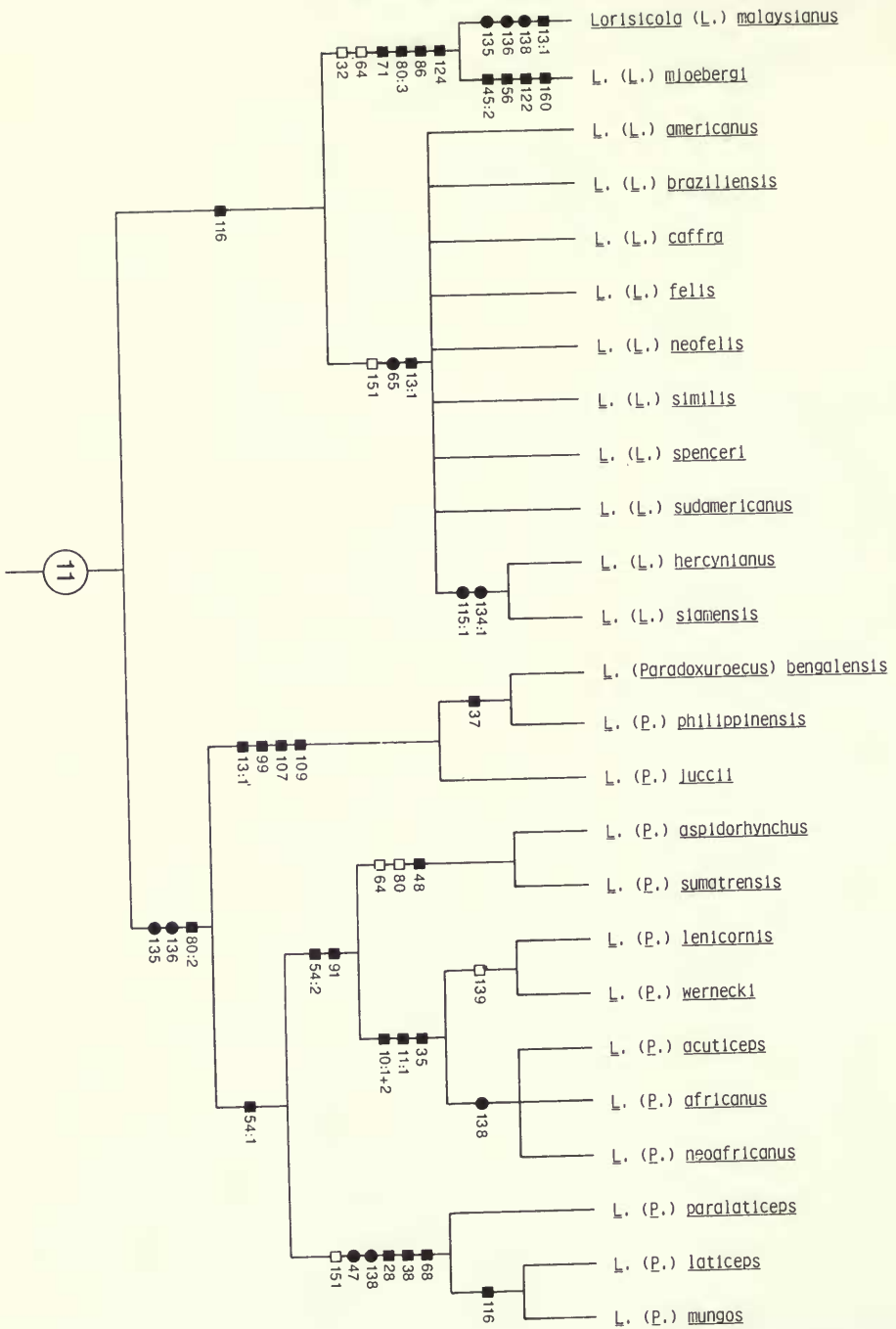


Fig. 33 Cladogram of *Loriscicola* (clade 11 of Fig. 23). For explanation of numbered apomorphies see text.

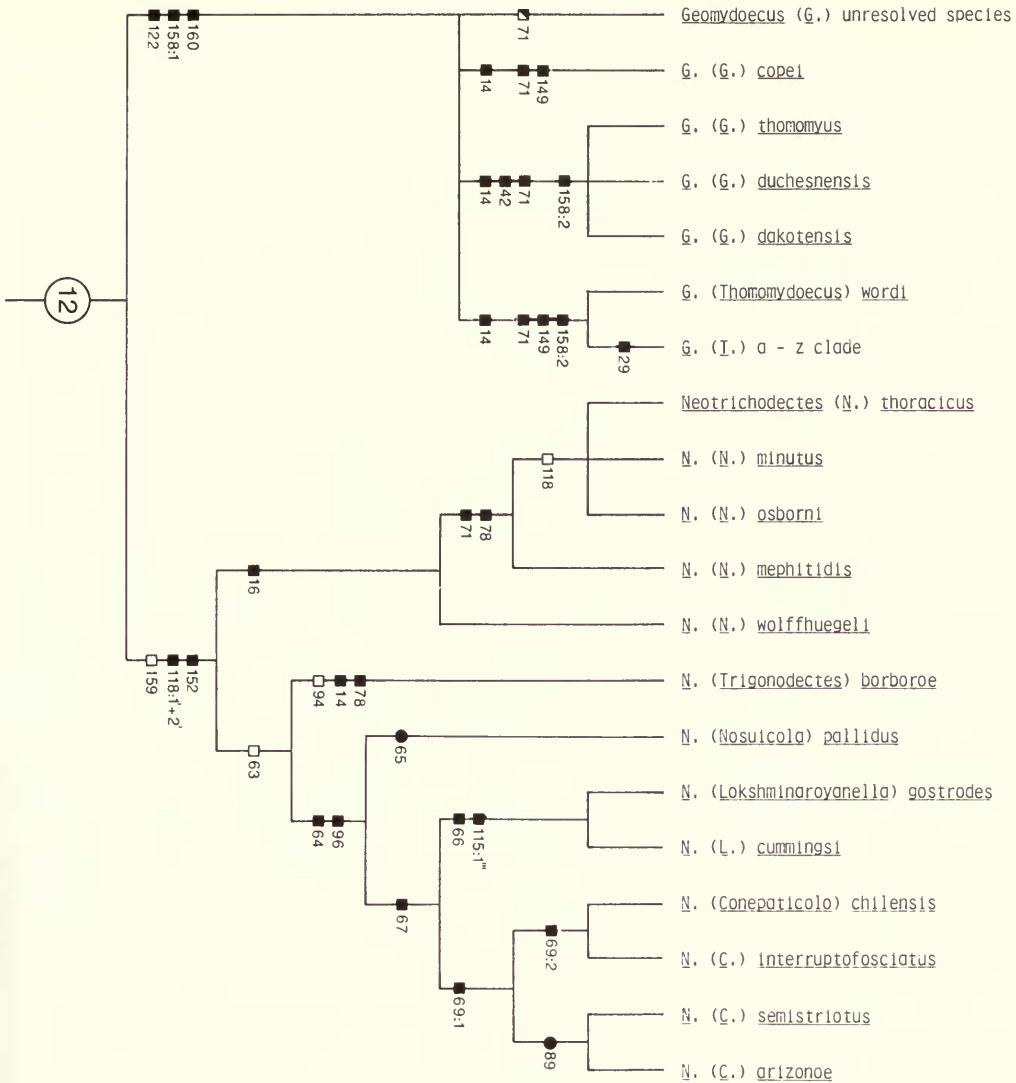


Fig. 34 Cladogram of Neotrichodectinae (clade 12 of Fig. 23: genera *Neotrichodectes* and *Geomydoecus*).

For explanation of numbered apomorphies see text.

been determined because of the poor state of preservation of the specimens, but its existence raises the possibility that character 20 is an apomorphy not of *Protelicola* but of only two species within the genus (the alternative being a reversal in the undescribed species). Character 20 is also homoplastically developed in *Felicola* and *Bovicola* (*Lepikentron*). If this character is disregarded, apomorphies 72 and 13:1 must be compared for their comparative likelihood of homoplasy. Apomorphy 13:1 is homoplastically developed at 22 other points on the cladogram whilst 72 is found elsewhere only in *Bovicola* (*Lepikentron*). Apomorphy 72 should clearly be given much more weight than 13:1 in construction of the cladogram, and 20 is considered of uncertain value in view of the undescribed species of *Protelicola*. For these reasons the cladogram is retained as proposed, even though it is not maximally parsimonious.

The dorsal projection of pleurum IV (character 159) is lost in the Trichodectini, but postulated as secondarily regained in *Werneckodectes* and *Trichodectes* (*Paratrichodectes*) *zorillae*. The form of the projection is different in the two species, however, which indicates the independent development of the structure.

Whilst the genus *Geomydoecus* s.l. is almost certainly holophyletic, this probably does not

apply to either of the two included subgenera (Fig. 34). The question of holophyly should be addressed first in the smaller subgenus *Geomydoecus* (*Thomomydoecus*). All but one of the included species (*G. (T.) wardi*) have characteristically asymmetric male genitalia (character 29), and are proposed on this basis to be a holophyletic group (the *asymmetricus*-*zacatecae* clade or 'a-z clade'). *G. (T.) wardi* and the a-z clade share the following apomorphies: posterolateral temple margin with single stout seta and associated shorter, finer setae (a character not included in the data matrix); male parameral plate apically pointed (character 14); gonapophysis smoothly continuous with ventral vulval margin (character 71); male abdominal terga II and III with median setal group comprising exceptionally long, stout setae (character 149); and pleural projections sclerotised, especially in females (character 158:2). The possession of a single stout temple seta is unique to these species, but may be a reduction from the two stout setae found in this position in some *Geomydoecus* (*Geomydoecus*). Apomorphies 14, 71 and 149 are also shared by *G. (G.) copei*, and this species has the mesomer arch and parameral plate very slender, approaching the shape of the genitalia of the a-z clade more closely than does *G. (T.) wardi*; the posterolateral temple margin lacks any specially-modified setae, but this may be due to secondary loss. Apomorphies 14, 71 and 158:2 are shared by the *G. (G.) thomomys-dakotensis* clade, but the male genitalia are considerably broader than those of *G. (T.) wardi*, and the mesomer arch lacks a median extension (an autapomorphy of the clade). This clade has a further autapomorphy in the form of the posterolateral setae of the temple margin, which comprise a single long fine seta and associated shorter fine setae. As with *G. (G.) copei*, the plesiomorphic form of the temple setae is unknown, and could have been the form found in *G. (Thomomydoecus)*. Other species of *G. (Geomydoecus)* have a single apex to the parameral plate (character 14), but do not share any of the other apomorphies mentioned. *G. (T.) wardi*, the a-z clade, and the *G. (G.) thomomys-dakotensis* clade are all parasitic on *Thomomys* spp., whilst *G. (G.) copei* is a parasite of *Orthogeomys hispidus*; both host genera are parasitised by other members of *Geomydoecus* (*Geomydoecus*).

The apomorphies listed above plainly do not support unequivocally any of the three possible sister-group relationships of the a-z clade without invoking homoplasy to an unjustifiable extent. It is apparent, however, that *G. (Geomydoecus)* is paraphyletic with respect to *G. (Thomomydoecus)* and that the latter subgenus is possibly polyphyletic. A full phylogenetic analysis of the 102 species and subspecies of *Geomydoecus*, which would have been necessary to resolve the problem, was not attempted. The hosts of the genus are all geomyid rodents, the systematic and taxonomic understanding of which is of questionable accuracy (Price, pers. comm.). For the purposes of this study the subgeneric concepts proposed by Price & Emerson (1972) are retained.

Taxonomic history of Trichodectidae

Burmeister (1838) divided the Mallophaga into two families, Liotheidae and Philopteridae, the latter comprising the two genera *Philopterus* and *Trichodectes*. Kellogg (1896) proposed the suborders Amblycera and Ischnocera for Liotheidae and Philopteridae (sensu Burmeister) respectively, and erected the family Trichodectidae for the genus *Trichodectes*.

Mjöberg (1910) described *Damalinia* and *Eutrichophilus*, the second and third genera of Trichodectidae, and Stobbe (1913a) described a fourth genus, *Eurytrichodectes*. Stobbe (1913b) revised the family for the first time. Ewing (1929) described four further genera and provided a key to all eight, although Ferris (1929) regarded Ewing's new genera as of 'most dubious value'. Bedford (1929, 1932a, 1932b, 1936) described a further 10 genera, two of which were junior synonyms of genera proposed by Ewing (1929), thus bringing the total to 16; Ewing (1936) provided a key to 14 of these. Kéler (1938a) recognised 24 genera, 10 of them new (although one of these had been published previously by Kéler, 1934 as a *nomen nudum*). The two genera omitted by Kéler (1938a) were the same two previously omitted by Ewing (*Cebidicola* Bedford, 1936 and *Loricicola* Bedford, 1936); the three species included in these genera were placed by Kéler with two others, also from primates, in his new genus *Meganarion* (although with the proviso 'without, of course, intending to establish the congeneric status of these species'). Kéler

(1938a) provided a key to most of the genera described in his paper (with the sole exception of *Meganarion*) and to many of the species. Werneck (1941) introduced the subgenus concept to the taxonomy of Trichodectidae, describing three new subgenera in two of the four genera of the family parasitic on hyraxes. During the decade following K  ler's (1938a) review of the family a number of new genera were described, bringing the total number of available names in the genus-group to 43 by the end of 1948. Werneck (1948, 1950) reviewed all the Trichodectidae, and recognised 20 genera (though one of these doubtfully) and three subgenera. No genera and only one subgenus have been described since 1948. The most recent name to be added (*Lakshminarayanelia* Eichler, 1982) was published as a replacement name for a junior homonym, and brings the total of available names to 45. There have been no revisionary works of the family since those of Werneck (1948, 1950), although Hopkins & Clay (1952), when cataloguing the 'Mallophaga', accepted 13 genera, some of these doubtfully, and Eichler (1963) recognised 38 genera (with no subgenera).

The problem of establishing criteria by which taxa can be distinguished at the generic level received early attention. An attempt to identify morphological characters for this purpose was initiated by Bedford (1929). Bedford (1932a) provided a more thorough discussion, and concluded that whilst the shape of the head, the presence or absence of abdominal sclerites and the form of the female gonapophyses were of value, the form of the male genitalia and the number of abdominal spiracles provided no useful guide. Ewing (1936) came to a quite different conclusion, regarding abdominal spiracle number as 'the most important generic character'. Bedford (1939) realised the unworkability of any system involving *a priori* assessment of morphological characters for generic discrimination, although he still felt that abdominal spiracle number was not of value at the generic level, and noted that (morphological) generic characters 'may not be very striking'. To supplement or replace morphological characters Bedford (1939) made use of host data, the possibility of which was first discussed by Kellogg (1913, 1914) and Harrison (1916b). Bedford (1939) wrote: 'Before placing a species in a new genus one should ask oneself: would it be possible to say from what kind of host the parasite was taken off had it not been recorded? If it is impossible to answer the question, then one should be justified in placing it in a new genus.' Hopkins (1941) used this principle to a certain extent in his discussion of *Felicola*. He also discussed the morphological characters used for the discrimination of the genus from others, and pointed out that 'the singling out of one character [on which to base genera] . . . only tends to obscure natural relationships'. Werneck (1936) perceived and treated the problem of generic discrimination in a rather different way from those described above. He noted that whilst the type-species (and sometimes a few species similar to the type) of each of the described genera were quite distinct, other species showed intermediate characters. The existence of these 'transitional forms' convinced Werneck that there was no validity in the separate genera, so he synonymised them all (with the exception of some genera not found in South America, which were outside the scope of the paper). Bedford (1939) regarded this action as 'unwarrantable' and reinstated all the genera. Hopkins (1942, 1943) reviewed the characters used to separate the genera of Trichodectidae parasitic on carnivores and antelopes respectively. In each case he found annectent species as described by Werneck (1936), and took similar action, though modified by the belief that louse genera should somehow reflect host taxa. Hopkins (1942) therefore accepted three genera of Trichodectidae parasitic on carnivores and later (1943) accepted one genus parasitic on antelopes. Werneck (1948, 1950), although less influenced by the host data, recognised more genera than had Hopkins. He accepted the morphologically 'distinct' species and species groups as genera, and placed annectent species in the genus which they most closely resembled. Hopkins (1949) 'conceded subgeneric status to many groups which seem likely to be accepted by systematists whose views . . . differ from mine' and recognised 14 genera and 20 subgenera. Hopkins & Clay (1952) synonymised some of the subgenera accepted by Hopkins (1949), but raised others to generic status. Ledger (1980) held views similar to Hopkins & Clay (1952), although in some cases followed the views of Hopkins (1949); the resultant generic arrangement still involved fewer genera than accepted by Werneck (1948, 1950), and many more subgenera. Emerson & Price (1981), however, could 'find no basis for rejecting the classification of Trichodectidae given by Werneck (1948, 1950)', and suggested

that the 'question of genera vs subgenera will perhaps continue until Mallophaga have been described from all likely hosts'. A number of other workers also follow these views. A third group of taxonomists (e.g. Eichler, 1963; Zlotorzyska, 1972) have accepted not only all the genera recognised by Werneck (1948, 1950), but also a number of genera that Werneck considered as junior synonyms; the subgenus category is not used, however. The present generic placement of most of the Trichodectidae is thus a matter of some contention and a review of the variations in status of some genera and subgenera is presented in Tables 3–5.

	Ewing (1936)	Kéler (1938a)	Eichler (1941)	Hopkins (1943)	Hopkins (1949)	Werneck (1950)	Hopkins & Clay (1952)	Eichler (1963)	Ledger (1980)	Emerson & Price (1981)	Present study
1. <i>Damalinea</i> Mjöberg, 1910	1	1	1	1	1	1	1	1	1	1	1
2. <i>Bovicola</i> Ewing, 1929	2	2	2	= 1	1 (2)	2	1 (2)	2	1 (2)	2	2
3. <i>Tricholipeurus</i> Bedford, 1929	3	3	3	= 1	1 (3)	3	1 (3)	3	1 (3)	3	1 (3)
4. <i>Cervicola</i> Kéler, 1938a	4	4	-	1 (4)	= 1	= 1 & = 2	4	= 1 s.l.	= 2	= 2	1 (4)
5. <i>Holakartikos</i> Kéler, 1938a	5	5	-	5	= 2	= 2	5	= 1 s.l.	= 2	= 2	2 (5)
6. <i>Lepikentron</i> Kéler, 1938a	6	6	-	6	= 2	1 (6)	6	= 1 s.l.	= 2	= 2	2 (6)
7. <i>Rhabdopedilon</i> Kéler, 1938a	7	7	-	1 (7)	= 2	= 6	7	= 1 s.l.	= 2	= 2	= 2
8. <i>Werneckiella</i> Eichler, 1940	8	-	1 (8)	= 2	= 2	8	= 1 s.l.	= 2	= 2	= 2	8
9. <i>B. (Spinibovicola)</i> subgen. n.											2 (9) [from 2]
10. <i>Bisonicola</i> gen. n.											10 [from 2]
11. <i>Tragulicola</i> gen. n.											11 [from 1]

Table 3 Generic concepts in the Bovicolinae. The genera included in the table are represented by numbers 1–11; '2' indicates that the genus (*Bovicola*) is given full generic status, '1(2)' indicates that the genus (*Bovicola*) is considered a subgenus (of *Damalinea*) and '= 1' indicates that the genus is considered as a junior synonym (of *Damalinea*). The generic name *Bovidoecus* Bedford, 1929 is omitted, as it was synonymised with *Bovicola* by Bedford (1932a) and has not since been used. There is no reference in the table to Werneck (1936), who treated all genera of Trichodectidae as synonyms of *Trichodectes*.

	Kéler (1938a)	Eichler (1941)	Hopkins (1942)	Werneck (1948)	Hopkins (1949)	Hopkins & Clay (1952)	Eichler (1963)	Ledger (1980)	Emerson & Price (1981)	Present study
1. <i>Trichodectes</i> Nitzsch, 1818	1	1	1	1	1	1	1	1	1	1
2. <i>Neotrichodectes</i> Ewing, 1929	2	2	= 1	2	1 (2)	1 (2)	2	1 (2)	2	2 [to Neotrichodectinae]
3. <i>Galictobius</i> Kéler, 1938b	3	3	= 1	= 1	1 (3)	= 1	3	= 1	= 1	= 1
4. <i>Lutridia</i> Kéler, 1938a	4	4	= 1	4	1 (4)	4	4	1 (4)	4	4
5. <i>Stachiella</i> Kéler, 1938a	5	5	= 1	5	1 (5)	1 (5)	5	1 (5)	5	1 (5)
6. <i>Ursodectes</i> Kéler, 1938a	6	6	= 1	= 1	1 (6)	= 1	6	= 1	= 1	= 1
7. <i>Potusadia</i> Conci, 1942				= 1	1 (7)	= 1	7	= 1	= 1	= 1
8. <i>Trigonodectes</i> Kéler, 1944				= 1	1 (8)	= 1	8	= 1	= 1	2 (8) [to Neotrichodectinae]
9. <i>Werneckodectes</i> Conci, 1946				= 1	1 (9)	= 1	9	= 1	= 1	9
10. <i>Neolutridia</i> gen. n.										10 [from 4]
11. <i>T. (Paratrichodectes)</i> subgen. n.										1 (11) [from 5]

Table 4 Generic concepts in the Trichodectini (plus *Neotrichodectes* and *Trigonodectes*). Coding as for Table 3. *Protelicola* is included in Table 5. The generic name *Grisonia* Kéler, 1938a is omitted and its replacement name, *Galictobius* Kéler, 1938b, used throughout.

	Bedford (1936)	Kéler (1938a)	Eichler (1941)	Hopkins (1941)	Werneck (1948)	Hopkins (1949)	Hopkins & Clay (1952)	Eichler (1963)	Ledger (1980)	Emerson & Price (1981)	Present study
1. <i>Felicola</i> Ewing, 1929	1	1	1	1	1	1	1	1	1	1	1
2. <i>Protelicola</i> Bedford, 1932	-	2	2	2	= 1	1 (2)	= 1	2	1 (2)	= 3	2 [to Trichodectini]
3. <i>Suricatoecus</i> Bedford, 1932	= 1	3	3	= 1	3	1 (3)	1 (3)	3	1 (3)	3	1 (3)
4. <i>Loristicola</i> Bedford, 1936	-	4	-	4	4	4	4	-	4	4	4
5. <i>Fastigatosculum</i> Kéler, 1939			5	= 1	= 3	-	= 3	5	= 1 s.l.	= 3	= 1
6. <i>Eichlerella</i> Conci, 1942					= 3	-	= 3	6	= 1 s.l.	= 3	= 3
7. <i>Paradozuroecus</i> Conci, 1942					= 1	-	= 1	7	= 1 s.l.	= 1	4 (?)
8. <i>Neofelicola</i> Werneck, 1948					8	1 (8)	1 (8)	8	1 (8)	8	= 7
9. <i>Parafelicola</i> Werneck, 1948					9	1 (9)	1 (9)	9	1 (9)	9	= 7

Table 5 Generic concepts in the Felicolini (plus *Protelicola*). Coding as for Table 3. The generic names *Bedfordia* and *Felicinia* (a junior homonym and an absolute synonym respectively) have not been included as their status has not varied; they are discussed in the comments following the description of *Felicola* s. str. below.

Hopkins (1941) presented an explanation for the presence of so many annectent species in the Trichodectidae and a justification for synonymising many of the genera, writing: 'I believe the explanation to be that the Trichodectidae are in the process of dividing up into genera; in some cases the divergence has proceeded far enough for us to recognise the segregates as generically distinct, but in a much greater number of cases extreme members of a group may have become strikingly distinct whilst the others remain as connecting-links which entirely undo our attempts to find characters peculiar to the group.' Hopkins' statement implies that the species in a genus are somehow evolving as a unit, and is linked to the typological approach to taxonomy. Relationships between three or more taxa, if assessed by a simple count of character states (i.e. not distinguishing between plesiomorphies, apomorphies and homoplasies) are frequently reticulate in aspect (Simpson, 1961; Hennig, 1966; Mayr, 1969). The greater the number of homoplasies the more complex the reticulum is likely to be, and the more difficult it is to combine the taxa into groups. If genera are constructed on this principle some morphologically distinct species and species-groups will be distinguished, 'linked' by annectent species, with the concomitant absence of 'gaps' between genera – precisely the problem with traditional groupings of the Trichodectidae. The 'problem' of annectent species is therefore engendered by the typological approach; the difficulties in distinguishing supra-specific groups are also a result of this, but combined in the Trichodectidae with a high degree of homoplasy.

The difficulties discussed above have discouraged authors from attempting to produce keys to genera of the Trichodectidae. Since the key to genera published by Kéler (1938a), very few have been published, and none included all the genera. Kéler (1944) produced a key to some genera, slightly emended from Kéler (1938a), but a promised second half to the paper containing the rest of the key was never published. Werneck (1948, 1950), despite describing all of the genera, did not attempt to produce a key. A few keys have since been published in faunistic works, for example Toulechkoff (1955) produced a key (in Bulgarian) to the genera found in Bulgaria, and Zlotorzyska (1972) published a rather inaccurate key (in Polish) to the genera found in Poland.

Although most authors follow Kellogg (1896) in their conception of the Trichodectidae, and retain familial rank for the group (e.g. Hopkins & Clay, 1952; Hopkins, 1960; Ledger, 1980; Emerson & Price, 1983), the rank of the group has been raised by others. Kéler (1938a) raised the Trichodectidae to superfamily level and included three families: Trichodectidae, Bovicolidae and Dasyonygidae, the latter two being described as new. In the Trichodectidae he placed four subfamilies, all of which he indicated to be new: Trichodectinae, Felicolinae, Eurytrichodectinae and, dubiously placed in this family, Eutrichophilinae (Fig. 35). Eichler (1940)

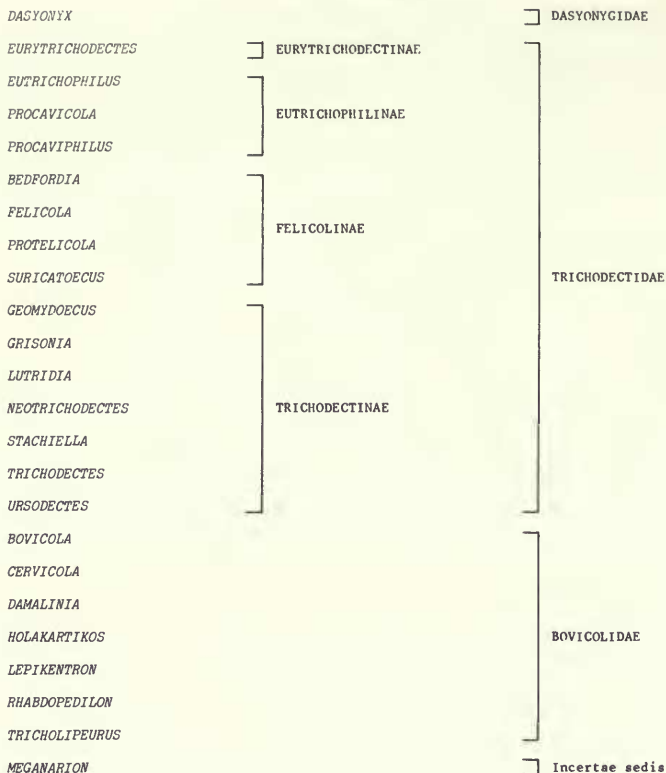


Fig. 35 Classification of 'Trichodectoidea' according to Kéler (1938a).

described two further subfamilies in the Trichodectidae (sensu Kéler, 1938a): Lymeoninae and Cebidicolinae. Eichler (1941) described the new subfamily Damaliniinae in the Bovicolidae, attributing the nominate subfamily to himself. He also transferred the Eurytrichodectinae and the Eutrichophilinae to the Dasyonygidae, again attributing the newly-defined nominate subfamily to himself. Eichler (1941) considered the rank of the whole group to be not superfamily but 'family group' and termed it the Trichodectiformia (attributed to Kéler, 1938a); the subfamily Trichodectinae is also attributed to Kéler (1938a) but the nominate family is attributed to Burmeister (1838). The classification proposed by Eichler (1941) is depicted in Fig. 36. Kéler (1944) retained the Eurytrichodectinae in Trichodectidae and moved the Eutrichophilinae to Bovicolidae; the subfamilies described by Eichler (1940, 1941) were not mentioned (Fig. 37). The Trichodectidae were attributed by Kéler (1944) to Kellogg (1896) but the nominate subfamily to Kéler (1938a). The superfamily rank was retained and the 'family group' not mentioned. Hopkins (1949) regarded the families proposed by Kéler (1938a) as subfamilies and the subfamilies as at most tribes. Hopkins also, following his synonymy of *Bovicola* with *Damalinia*, considered that 'Bovicolinae must be known as Damaliniinae'. Eichler (1963) retained the higher ranks and included 'interfamilia Trichodectiformia' within the superfamily Trichodectoidea. He moved the Lymeoninae to Dasyonygidae (wherein he retained Eurytrichodectinae), but accepted the move of Eutrichophilinae to Bovicolidae proposed by Kéler (1944). Eichler (1963) also proposed the division of the Trichodect(oidea) into tribes, indicating their existence and composition by variations in typography in the list of genera presented (Eichler, 1963: 159, lines 31–37). Eichler (1963) did not publish any of the tribal names, but Lakshminarayana (1976) listed all of them. Neither Eichler (1963) nor Lakshminarayana (1976), however, gave any statement that purported 'to give characters differentiating the tax(a); or . . . a definite bibliographic reference to such a statement' as is required by the *International Code of Zoological Nomenclature* for any name published after 1930 (Article 13).

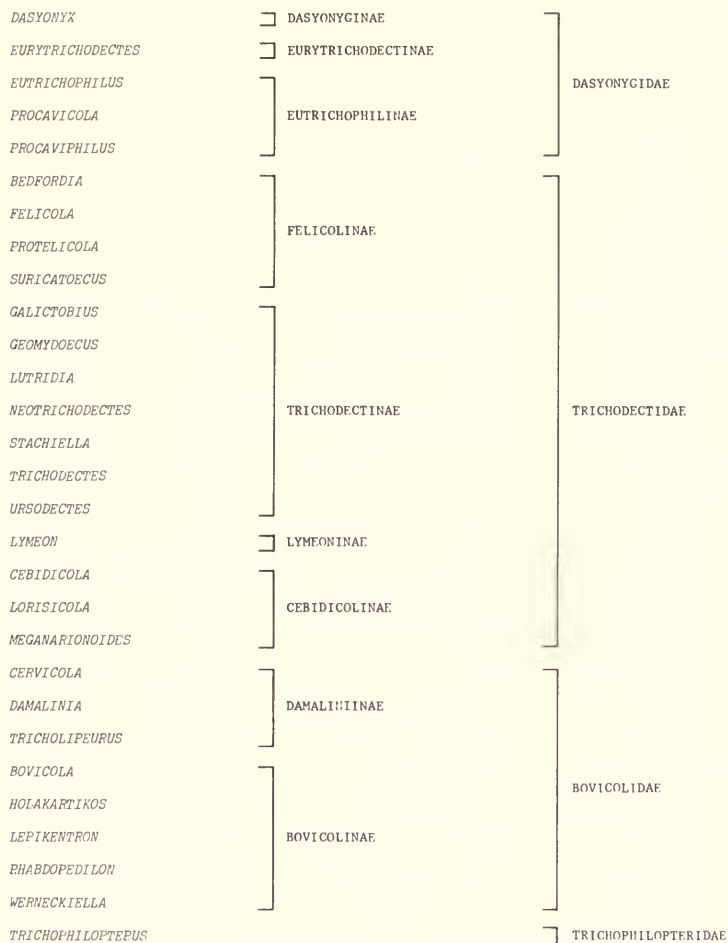


Fig. 36 Classification of 'Trichodectiformia' according to Eichler (1941).

None of the (11) names, therefore, are available for taxonomic use. Eichler (1963) attributed Trichodectoidea, Trichodectiformia, Trichodectidae and Trichodectinae to Burmeister (1838) but, whilst (correctly) attributing Bovicolidae and Dasyonygidae to Kéler (1938a) he attributed the nominate subfamilies of both to Eichler (1941). The classification proposed by Eichler (1963) is depicted in Fig. 38. Kéler (1969) proposed a classification similar to that proposed by Kéler (1944), but omitting a number of genera (Fig. 39).

Article 36 of the *International Code of Zoological Nomenclature* (1984) states that all categories in the family-group (tribe, subfamily, family, superfamily and any supplementary categories, according to Article 35a) are co-ordinate, and a name established for any category within the group is available with its original date and author for a taxon with the same type genus in each of the categories. The Trichodectinae, Trichodectidae, Trichodectiformia and Trichodectoidea should therefore all have the same date and author. The first use of a family-group name based on the type genus *Trichodectes* was by Kellogg (1896), who ranked 'the Nitzschian families as suborders, the Nitzschian genera as families, and the Nitzschian subgenera, the genera of present-day writers, as genera.' Kellogg (1908) attributed the Trichodectinae (the only subfamily included in the Trichodectidae, which bore no attribution) to 'Burmeister (?)'. As explained above, subsequent attribution has frequently been to Burmeister (1838) and, in the case of some co-ordinate names, to Kéler (1938a). Burmeister (1838) did not mention any taxon in the family-group with the type genus *Trichodectes*. All

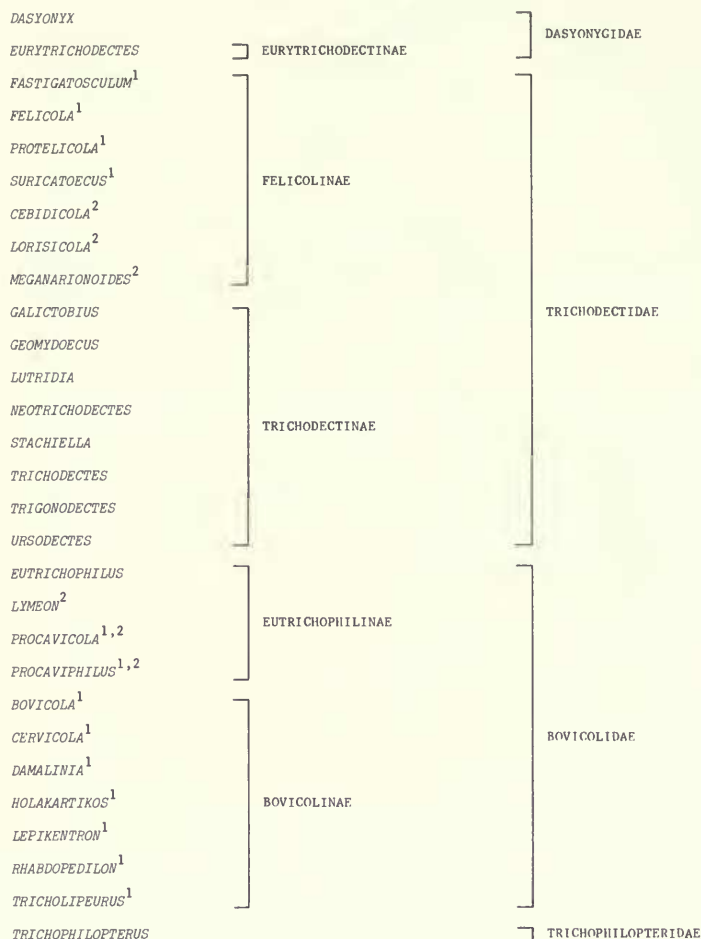


Fig. 37 Classification of 'Trichodectoidea' according to Kéler (1944). ¹Position of genus inferred from Kéler (1938a). ²Position of genus inferred from key in Kéler (1944).

family-group names with the type genus *Trichodectes* should therefore be attributed to Kellogg (1896). Trichodectidae Kellogg, 1896 has been placed on the Official List of Family-group Names in Zoology (Opinion 627, *Bull. zool. Nom.* 19: 91–96, (1962)). The names Bovicolinae, Bovicolidae, Dasyonyginae and Dasyonygidae should all be attributed to Kéler (1938a), not Eichler (1941). The action of Hopkins (1949) is synonymising the senior family-group (Bovicolinae) with the junior (Damaliniinae) was taken because he believed *Bovicola* and *Damalinia* (the type-genera) to be synonyms, and *Damalinia* is senior to *Bovicola*. This action is incorrect under Article 40 of the *Code*, however, which states that, at least after 1961, in the case of type-genus synonymy the senior family-group name is to be used for the family-group taxon that contains both senior and junior synonyms. This Rule can be set aside for such an action if taken before 1961, if the name has 'won general acceptance' (Article 40b). The subfamily Damaliniinae sensu Hopkins (1949) has rarely if ever been used since, whilst the name Bovicolidae (= Damaliniinae sensu Hopkins) has been employed by Eichler (1963) and Kéler (1969). The action of Hopkins (1949) is therefore rejected.

Kéler (1944) included the Trichophilopteridae – a family containing a single genus, parasitic on Lemurs – within the Trichodectoidea, although Kéler (1969) referred this family to the Philopteroidea. Eichler (1963) retained the Trichophilopteridae in the Trichodectoidea, but distinguished it as 'interfamily Trichophilopteriformia' as opposed to 'interfamily Trichodectiformia'. Stobbe (1913a), Ferris (1933) and Werneck (1948) all considered the affinities of

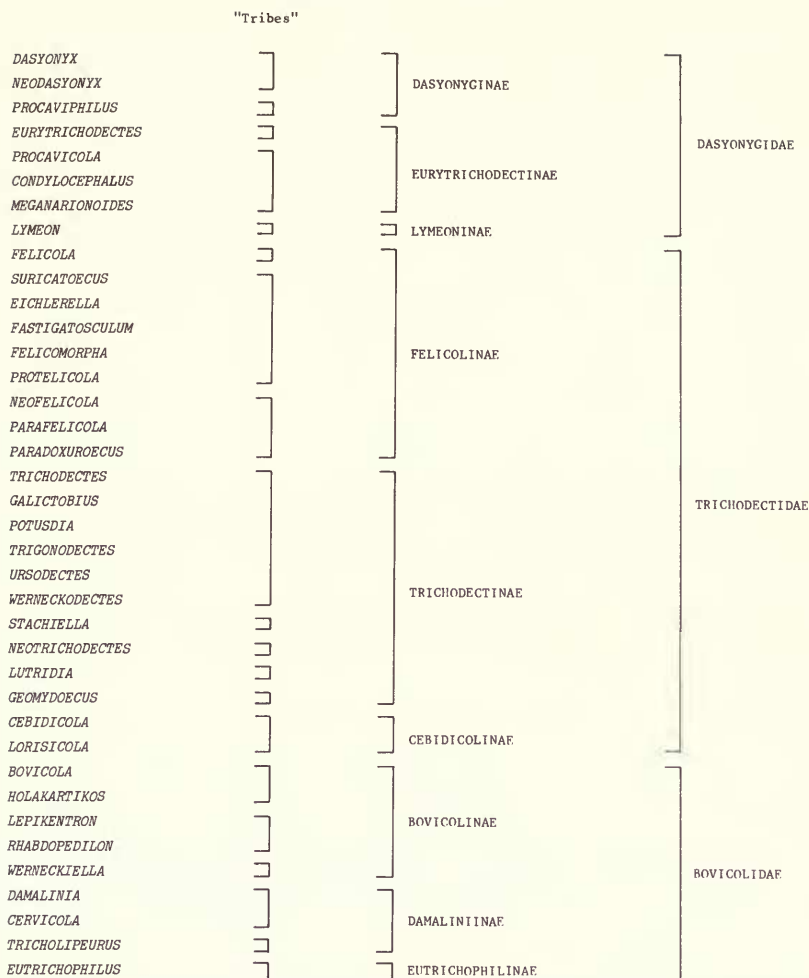


Fig. 38 Classification of 'Trichodectiformia' according to Eichler (1963). The 'tribes' are indicated by square brackets in the appropriate column, the first genus in each 'tribe' being intended by Eichler (1963) as the type-genus. See text.

Trichophilopterus to lie with the 'Phloptoridae' rather than with the Trichodectidae. In this study no apomorphies were found to indicate a sister-group relationship between *Trichophilopterus* and all or part of the Trichodectidae.

Proposed classification

The proposed classification is derived from the results of a cladistic analysis of the Trichodectidae (Trichodectiformia sensu Eichler, 1963) at the species level (Figs 23–34). The species are grouped on the four criteria discussed below, and ranked according to the principles of phyletic sequencing.

Holophyly. The classification includes, as far as possible, only holophyletic groups. Some genera and subgenera, however, may be found not to follow this criterion (see discussion of *Damalinia* s. str., *Dasyonyx* and *Geomydoecus* below).

Utility. Genera are ideally of 'moderate' size and relative morphological uniformity. If a genus is large and diverse, recognition is difficult and useful discussion on many aspects of biology or distribution prohibited; if genera are too small, identification is time-consuming and discussion

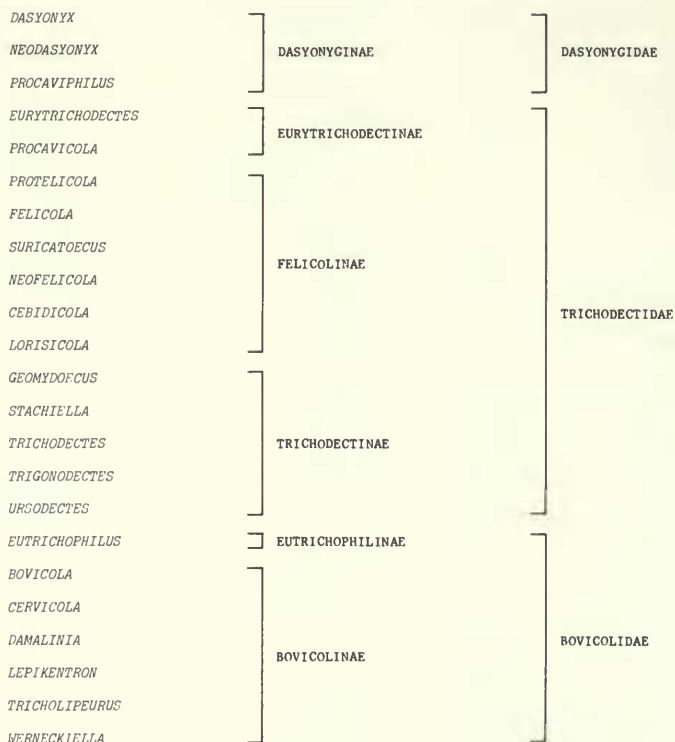


Fig. 39 Classification of 'Trichodectoidea' according to Kéler (1969).

again impeded. No 'absolute' size can be recommended, however, as the most satisfactory size will depend on a number of properties of the species, and must (in this study) conform to such limitations as are imposed by the criterion of holophyly. Subfamilies are chosen in this study to aid discussion by providing names for holophyletic groups of genera, and to fulfil the logic of the phyletic sequencing convention.

Stability. To ensure that the classification has maximal stability the generic concepts accepted in this study conflict as little as possible with established usage.

Distinctness. To facilitate identification, taxa in the genus-group should be as distinct from one another as possible. The requirements of Mayr (1969) that genera must be separated by a decided gap, and that the 'size' of the gap should be inversely proportional to the size of the taxon, are not necessarily compatible with the criterion of holophyly followed here, however, and the problem of annectant species (that 'fill' any such gap) has been discussed above. Despite the apparent drawback of adherence to holophyletic groups at the expense of inter-generic 'gaps', it has been possible in this study to produce a key to the genera of Trichodectidae (see discussion of keys to genera of Trichodectidae above).

The formation of the genera of Trichodectidae is discussed below, to give an indication of the rationale behind each decision. The genera are discussed by subfamily, and the division into subfamilies is discussed last.

Bovicolinae (Figs 24–27, 40)

This clade was not resolved fully in the analysis, and a primary pentachotomy was obtained. The clade has been treated as a single genus (see Table 4), but the diversity of morphology and of hosts indicates that this concept is too broad to be of great value. Subdivision of the clade into smaller holophyletic groups increases the value of the classification for information retrieval, and leads to the acceptance of genera that approach the concepts of Werneck (1950). To obtain a

measure of conformity each of the five branches of the clade has been accorded generic status.

The monobasic genera *Bisonicola* and *Tragulicola* require no comment, and the genus *Werneckiella* was revised by Moreby (1978). Of the two remaining clades, one corresponds approximately to a restricted concept of *Bovicola*, the other to *Damalinia* plus *Tricholipeurus* (sensu Werneck, 1950). The *Bovicola* clade (genus *Bovicola*) has a primary tetrachotomy, with most of the species belonging to only one of the four resultant clades (Fig. 24). The species in this large clade are morphologically more similar to one another than they are to any of the species in the other three clades. To recognise this morphological divergence (and thus facilitate identification), and to demonstrate in the classification the extent of the phylogenetic knowledge, the four branches are each accorded subgeneric status. The *Damalinia* plus *Tricholipeurus* clade (genus *Damalinia*) has a primary trichotomy (Fig. 23), and it is clear that discussion of the genus will be facilitated by the recognition of each of these branches as a subgenus. *Damalinia* s. str. comprises two major clades, each characterised by the form of an apomorphic development of abdominal pleurum II onto the sternum. As discussed above, these two forms may be co-apomorphies, or may represent two states in a transformation series. If the latter interpretation is correct, one of the clades is probably paraphyletic with respect to the other.

Eutrichophilinae

Only the single genus *Eutrichophilus* is included, with no change in generic concept.

Dasyonyginae (Figs 28, 29)

The previously-accepted generic concepts in this subfamily remain essentially unchanged at the subgenus level. The only change is the transfer of the subgenus *Meganarionoides* from *Procaviphilus* to *Procaviphilus scleroticus* and *P. serraticus* in *P. (Meganarionoides)*. Subgenera are used (as in Werneck, 1941, 1950; Ledger, 1980) as no advantage accrues from regarding each of the clades so recognised as a full genus, and application of the principles of phyletic sequencing allows retention of all the currently-used generic and subgeneric names with no higher taxa required, whereas recognition of all these as genera would require the description of a number of intercalating family-group taxa.

It is notable that one of the two subgenera of *Dasyonyx* may be paraphyletic with respect to the other, as the subgenera are characterised by apomorphic developments of the teeth of the tarsal claws. These may be co-apomorphies or two states in a transformation series (see above). If the latter interpretation is correct, one of the subgenera is probably paraphyletic with respect to the other.

Trichodectinae (Figs 23, 30–33, 40)

The first dichotomy in this clade splits it roughly into *Felicola* (sensu Ledger, 1980, but without *Protelicola* and with *Lorisicola*) on one side and *Trichodectes* (sensu Ledger, 1980, but without *Neotrichodectes* and *Trigonodectes*, and with *Protelicola*) on the other. The diversity of morphology of the lice, and the variety of hosts infested, indicates that the very broad generic concepts endorsed by Ledger (1980) are too inclusive to be of great value in data-retrieval and discussion. For this reason the genera proposed here are smaller than those of Ledger (1980) and, in some cases, approach the concepts held by Werneck (1948).

Most of the species in the *Trichodectes* side of the initial dichotomy arise from the three branches of an apical trichotomy (Figs 30, 31). The branch of this trichotomy comprising the *pinguis-galictidis* clade corresponds roughly to the concept of *Trichodectes* held by Werneck (1948), whilst the other two branches (the *ovalis-zorillae* clade and the *emeryi-potus* clade) correspond roughly to *Stachiella* sensu Werneck (1948) (though *fallax*, *octomaculatus* and *potus* were placed in *Trichodectes* by Werneck, 1948). However, placing two of the three clades of the trichotomy in a taxon *Stachiella* and excluding the third results in a group that is not holophyletic. Recognising each of the three branches of the trichotomy as a separate genus is undesirable, as the three intergrade phenetically. The course followed here is to recognise the

genus *Trichodectes* comprising all three branches, each of these being considered a subgenus (Fig. 40). Using the principle of phyletic sequencing the sister-group of *Trichodectes* is also considered a genus, for which the name *Werneckodectes* is available. Likewise the next three branches of this clade are also considered genera. This process necessitates dividing Werneck's genus *Lutridia* into two genera, but retention of the genus as it stood calls for recognition of a paraphyletic group in the classification, and, although the species in the two clades comprising *Lutridia* (sensu Werneck, 1948) are superficially similar, some of these similarities may be homoplastic.

The other branch of the initial dichotomy of the Trichodectinae clade comprises, as noted above, most of the species consigned to *Felicola* by Ledger (1980) plus the single species of the genus *Loriscicola* (sensu Werneck, 1950). The two branches of this clade (Fig. 23) are each considered as genera which, taking the most senior available names, are known as *Felicola* and *Loriscicola*. For reasons of utility, each genus is divided into two holophyletic subgenera. None of the genera or subgenera coincides with any previous generic concept, as such concepts relied heavily on head shape and abdominal spiracle number, both of which characters have proved to be subject to a considerable degree of homoplasy.

In order to maintain the logic of phyletic sequencing, if the *Felicola*–*Loriscicola* clade is to be considered as comprising two genera, the rank of this clade and of the *Trichodectes*–*Protelicola* clade must be equal and formally recognised. Use of the tribal category permits this, and the family-group names Trichodectini and Felicolini are available (see full classification below). It must be stressed that these tribes are inserted to maintain the formal structure of the classification, and are not intended (or believed) to have any other significance.

Neotrichodectinae (Fig. 34)

The first dichotomy in this subfamily divides the clade into those species previously assigned to the genus *Geomydoecus* on one side, and species from *Neotrichodectes*, *Lakshminarayanella* and *Trichodectes* (sensu Werneck, 1948) on the other. The two branches will be discussed separately.

The genus *Geomydoecus* as previously recognised is fairly uniform in morphology, distribution and host species, and may be identified readily. To divide this genus into others would inhibit rather than encourage discussion, and the genus is retained in its present form. The two subgenera as proposed by Price & Emerson (1972) are also retained though, as indicated above, neither are holophyletic groups.

The other branch of the primary dichotomy comprises the 10 species previously assigned to the genus *Neotrichodectes* (considered a subgenus of *Trichodectes* by Hopkins, 1949 and Ledger, 1980), the two species previously assigned to the genus *Lakshminarayanella* (formerly *Lymeon*), and a single species formerly placed in *Trichodectes* by most authors (*T. barbarae*). The clade is plainly close to the established concept of *Neotrichodectes*, and it is preferable that this name is applied to as much of the group as possible. The 10 species of *Neotrichodectes* auctt. do not form a holophyletic group, however, though morphologically they are quite uniform. Inclusion of *T. barbarae* is unlikely to create problems, but *Lakshminarayanella* (as *Lymeon*) has been placed by some authors in a subfamily of its own (Eichler, 1940, 1963), and considered close to the hyrax lice (Kéler, 1944; Hopkins, 1949; Eichler, 1963). If *Lakshminarayanella* is synonymised with *Neotrichodectes* and given no formal recognition it is likely to be raised from synonymy by future workers because of its distinctive morphology, leaving *Neotrichodectes* paraphyletic. The course taken here is to recognise *Lakshminarayanella* as a subgenus of *Neotrichodectes*, which necessitates recognition of four other (holophyletic) subgenera, names already being available for two of these. Application of the principles of phyletic sequencing permits equal ranking of the subgenera within the genus.

Subfamilies (Fig. 40)

To divide the family into 'manageable' holophyletic groups for the purposes of discussion and to maintain the logic of phyletic sequencing, supra-generic groupings had to be employed. Use of

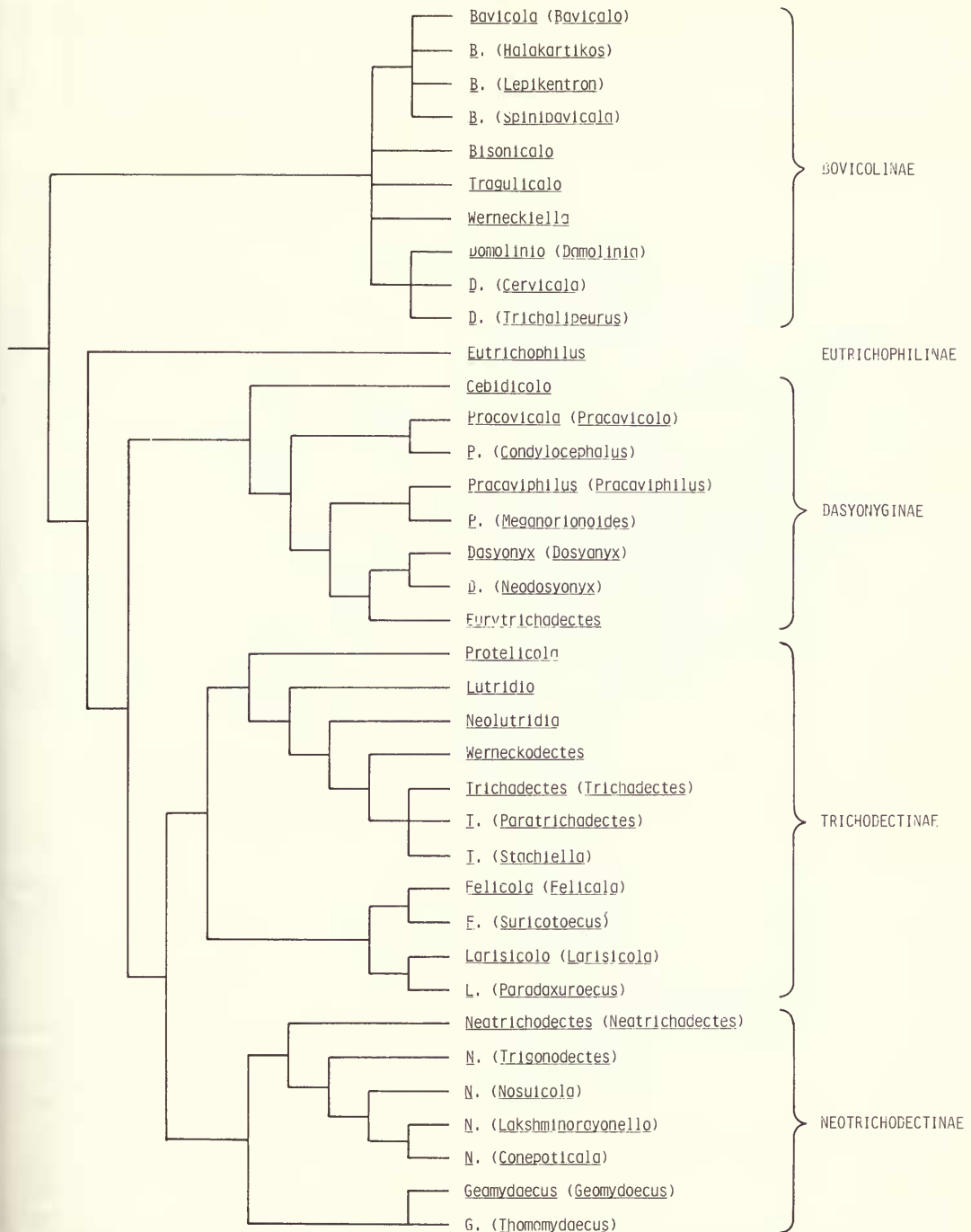


Fig. 40 Cladogram of the genera and subgenera of Trichodectidae, with subfamily assignments.

the principles of phyletic sequencing permitted the use of the subfamily category throughout (with the addition of the tribes mentioned above). The limits of the subfamilies were chosen for maximum utility, modified by the dictates of the sequencing convention. It would be surprising, given the high degree of homoplasy of structures in the Trichodectidae, if the subfamilies fulfilled the criterion 'distinctness' described above and were readily distinguishable. A key to

subfamilies is provided, however, largely to satisfy the requirements of the *International Code of Zoological Nomenclature* (Article 13) for a description to accompany any new name for, although names were available for most of the subfamilies, a single new name is required.

A complete classification of the Trichodectidae to generic level is set out below in phyletic sequence (as recommended by Wiley, 1979, 1981).

Sequenced classification of the Trichodectidae

Family TRICHOECTIDAE Kellogg, 1896

Subfamily BOVICOLINAE Kéler, 1938 (all genera *sedis mutabilis*)

Genus *BOVICOLA* Ewing, 1929 (all subgenera *sedis mutabilis*)

Subgenus *BOVICOLA* Ewing, 1929

Subgenus *HOLAKARTIKOS* Kéler, 1938

Subgenus *LEPIKENTRON* Kéler, 1938

Subgenus *SPINIBOVICOLA* subgen. n.

Genus *BISONICOLA* gen. n.

Genus *WERNECKIELLA* Eichler, 1940

Genus *TRAGULICOLA* gen. n.

Genus *DAMALINIA* Mjöberg, 1910 (all subgenera *sedis mutabilis*)

Subgenus *DAMALINIA* Mjöberg, 1910

Subgenus *CERVICOLA* Kéler, 1938

Subgenus *TRICHOLIPEURUS* Bedford, 1929

Subfamily EUTRICHOPHILINAE Kéler, 1938

Genus *EUTRICHOPHILUS* Mjöberg, 1910

Subfamily DASYONYGINAE Kéler, 1938

Genus *CEBIDICOLA* Bedford, 1936

Genus *PROCAVICOLA* Bedford, 1932

Subgenus *PROCAVICOLA* Bedford, 1932

Subgenus *CONDYLOCEPHALUS* Werneck, 1941

Genus *PROCAVIPHILUS* Bedford, 1932

Subgenus *PROCAVIPHILUS* Bedford, 1932

Subgenus *MEGANARIONOIDES* Eichler, 1940

Genus *DASYONYX* Bedford, 1932

Subgenus *DASYONYX* Bedford, 1932

Subgenus *NEODASYONYX* Werneck, 1941

Genus *EURYTRICHOECTES* Stobbe, 1913

Subfamily TRICHOECTINAE Kellogg, 1896

Tribe TRICHOECTINI Kellogg, 1896

Genus *PROTELICOLA* Bedford, 1932

Genus *LUTRIDIA* Kéler, 1938

Genus *NEOLUTRIDIA* gen. n.

Genus *WERNECKODECTES* Conci, 1946

Genus *TRICHOECTES* Nitzsch, 1818 (all subgenera *sedis mutabilis*)

Subgenus *TRICHOECTES* Nitzsch, 1818

Subgenus *PARATRICHOECTES* subgen. n.

Subgenus *STACHIELLA* Kéler, 1938

Tribe FELICOLINI Kéler, 1938

Genus *FELICOLA* Ewing, 1929

Subgenus *FELICOLA* Ewing, 1929

Subgenus *SURICATOECUS* Bedford, 1932

Genus *LORISICOLA* Bedford, 1936

Subgenus *LORISICOLA* Bedford, 1936

Subgenus *PARADOXUROECUS* Conci, 1942

Subfamily NEOTRICHODECTINAE subfam. n.

Genus *NEOTRICHODECTES* Ewing, 1929

Subgenus *NEOTRICHODECTES* Ewing, 1929

Subgenus *TRIGONODECTES* Kéler, 1944

Subgenus *NASUICOLA* subgen. n.

Subgenus *LAKSHMINARAYANELLA* Eichler, 1982

Subgenus *CONEPATICOLA* subgen. n.

Genus *GEOMYDOECUS* Ewing, 1929

Subgenus *GEOMYDOECUS* Ewing, 1929 (paraphyletic)

Subgenus *THOMOMYDOECUS* Price & Emerson, 1972 (polyphyletic?)

Descriptions of genera and subgenera

The generic and subgeneric descriptions below are arranged by subfamily in the order of the sequenced classification of the Trichodectidae (see above).

Descriptions are set out in the following order: paragraph one – head, both sexes, with details of sexually-dimorphic features of antennae, if present; paragraph two – thorax, both sexes, omitting mention of the anterior setae (on the post-temporal margin) which are present in all species; paragraph three – abdomen, both sexes, with details of sexually-dimorphic features of the setae, sclerites or shape, if present; fourth paragraph – female terminalia and genitalia; fifth paragraph – male subgenital plate, terminalia and genitalia. Descriptions are given of each genus as a whole, even where subgenera are present. The descriptions of subgenera (if any are present) follow that of the genus in which they are placed, and give only subgeneric characters, so that some of the paragraphs listed above may be omitted. Characters that vary between subgenera, if mentioned in the generic description, are indicated by an asterisk (*).

Each description is followed by an indication of the host group or groups parasitised, and by any pertinent comments on the taxonomy, morphology or biology of some or all of the included species. A check-list of all species included in each genus or subgenus is also given, the names being placed in alphabetical order. Following each species name in the check-lists is an indication of the number of specimens of each sex examined in the study.

Two species have not been placed, and are considered *incertae sedis*. *Trichodectes baculus* Schömmer, 1913; type-host: *Capra hircus* Linnaeus. *Trichodectes tigris* Ponton, 1870; type-host: *Felis tigris* Linnaeus. These species are discussed by Werneck (1950).

The subfamilies, genera and subgenera are keyed (p. 335).

BOVICOLINAE Kéler

Genus *BOVICOLA* Ewing

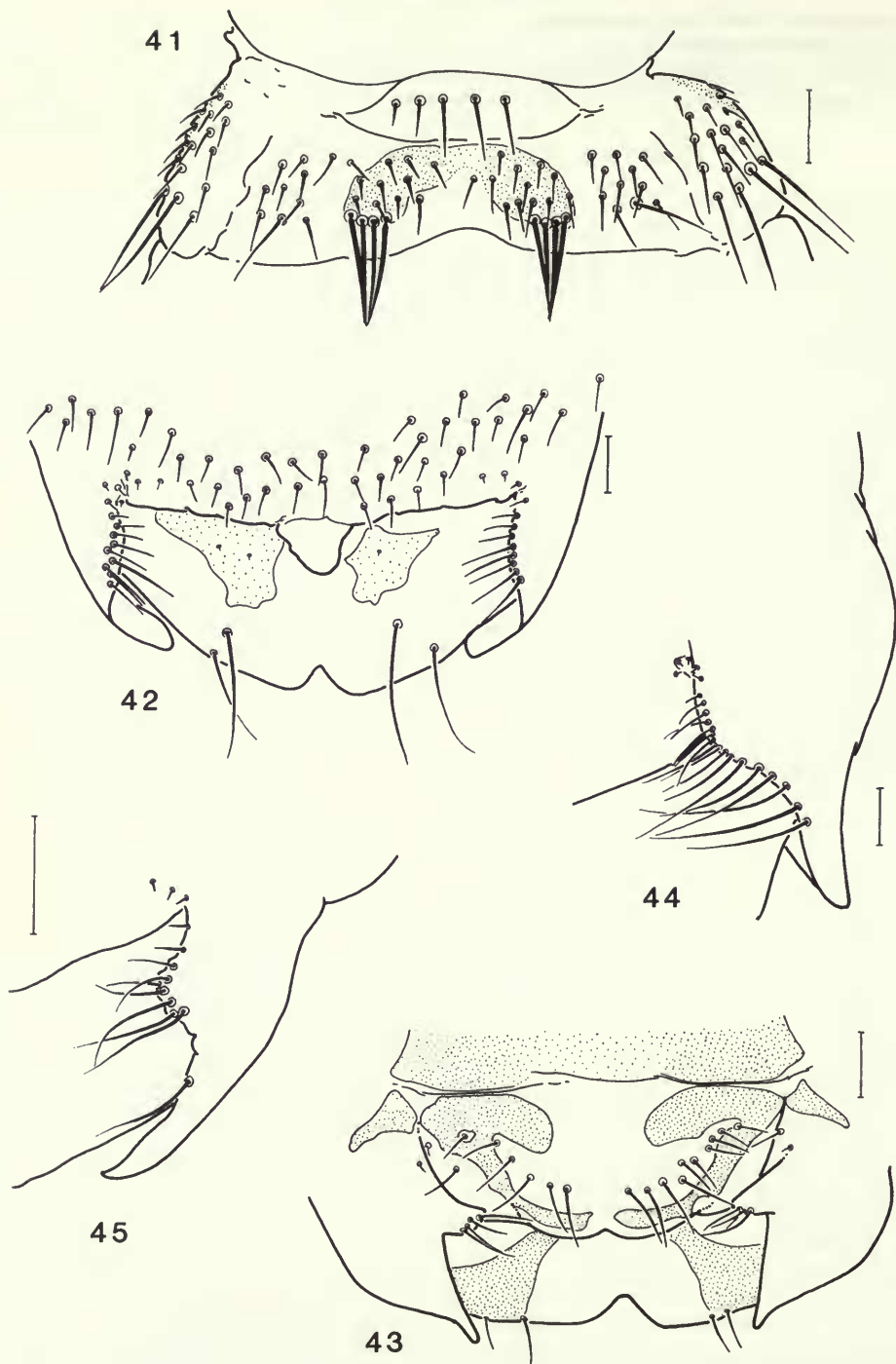
The genus *Bovicola* comprises four subgenera.

DESCRIPTION. Anterior of head with osculum absent or, if present, broad and shallow*; pulvinus of normal length or short and not attaining anterior margin of head; dorsal preantennal sulcus present or absent*; clypeal marginal carina not or only slightly broadened medially, or broadened to variable degree into bar with posterior and anterior margins roughly parallel, bar either straight and at right angles to long axis of head or curved and parallel to anterior margin of head*; anterolateral margin of head smoothly rounded; preantennal portion of head short, outline broadly rounded or trapezoid*. Temple margin smoothly convex or with posterior projection*, sometimes convexly produced posteriad*. Male scape expanded or not expanded*, with setal row apparently present or setae randomly scattered; flagellomeres fused in males and females; male flagellum with two basally-articulated 'teeth' and interior face not 'roughened'. Dorsum of head with more or less abundant setae, short, long or of moderate length*. Sitophore sclerite unmodified or with posterior arms extended*.

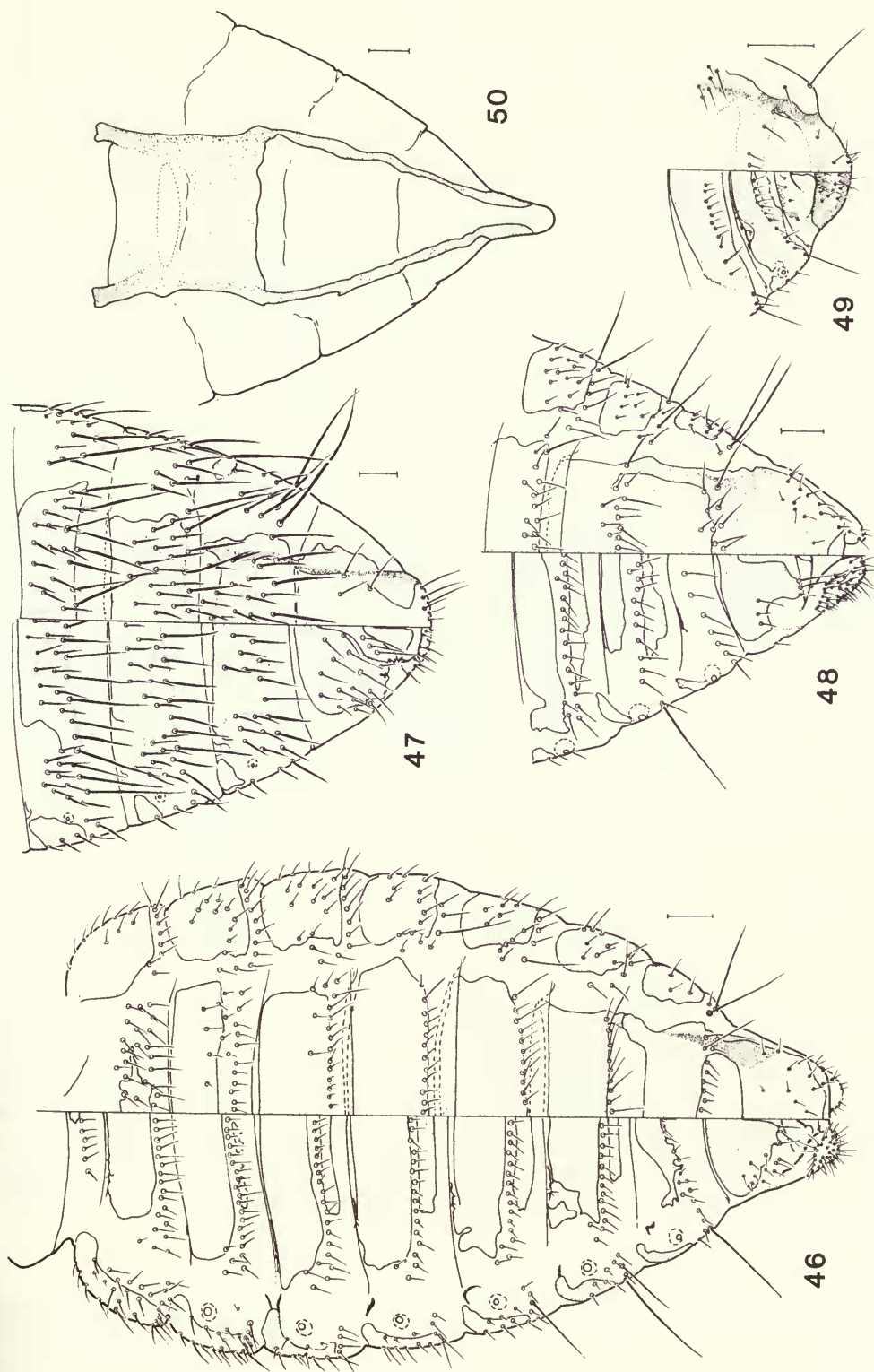
Thorax with more or less abundant setae, short, long, or of moderate length, frequently longest on postero-lateral margin of pterothorax*.

Abdomen oval or elongate, frequently tapering posteriorly more in male than in female*. Abdominal spiracles present on segments III–VIII. Abdominal setae variable*; anterior setae always present on pleura, sometimes on sterna and terga; postero-lateral setae absent. Abdominal pleural projections absent. Sclerites present at least on sterna III–VII (males) and III–VIII (females), terga II–VII (males) and III–IX (females) and pleura II–VIII; male terga with posterior sclerites present or absent*.

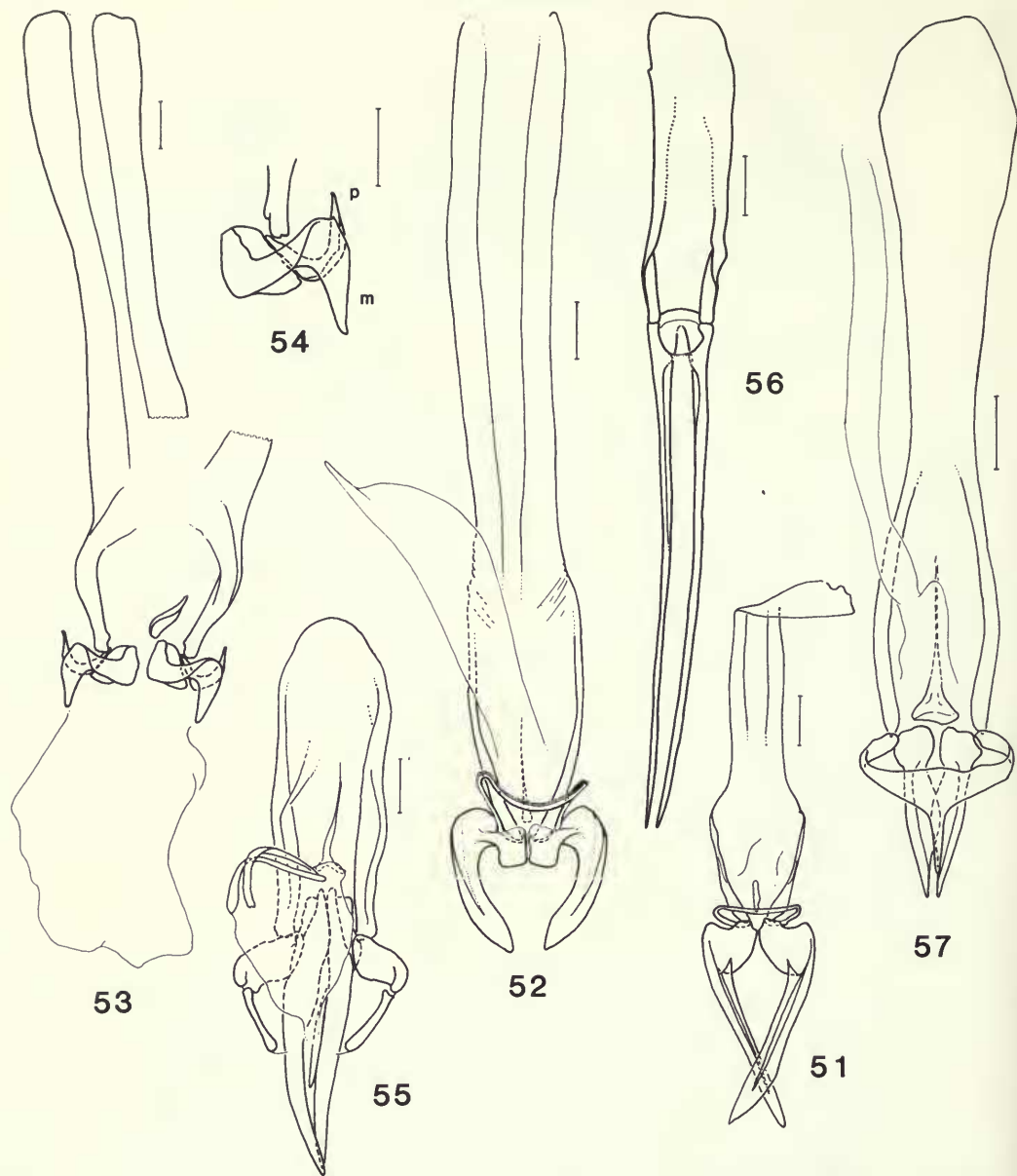
Gonapophyses with marginal setae; ventral lobe present, though sometimes not pronounced*. Gonapophyses meet ventral vulval margin acutely, not linked by sclerotised band. Ventral vulval margin not sclerotised, or sclerotised only medially; subgenital lobe absent, though small median membranous projection may be present (Fig. 42)*. Genital chamber sometimes with median antero-dorsal area lacking scales or spicules*.



Figs 41–45 *Bovicola* species. 41, *B. (Spinibovicola) hemitrangi*, ♂ abdominal terga I and II. 42, *B. (B.) jellisoni*, ♀ terminalia, ventral. 43, *B. (Lepikentron) breviceps*, ♀ terminalia, ventral. 44, *B. (Holakartikos) crassipes*, ♀ gonapophysis, ventral. 45, *B. (B.) caprae*, ♀ gonapophysis, ventral.



Figs 46-50 *Bovicola* species. 46, *B. (B.) caprae*, ♂ abdomen. 47-49, male terminalia of (47) *B. (Holakarikos) crassipes*; (48) *B. (B.) bovis*; (49) *B. (B.) concavifrons*. 50, *B. (Spinibovicola) hemiragi*, ♂ subgenital plate, setae omitted.



Figs 51–57 *Bovicola* species, ♂ genitalia. 51, *B. (B.) bovis*. 52, *B. (B.) caprae*. 53, *B. (B.) concavifrons*. 54, *B. (B.) concavifrons*, detail of right paramere (p) and mesomere (m). 55, *B. (Lepikentron) breviceps*. 56, *B. (Spinibovicola) hemitrangi*. 57, *B. (Holakartikos) crassipes*.

Male subgenital plate variable*. Pseudostyli present or absent*. Male genital opening dorsal or postero-dorsal. Male genitalia variable*.

Hosts. Bovidae, Cervidae and Camelidae (Artiodactyla).

COMMENTS. Some species of *Bovicola* are parthenogenetic, males being rare or unknown.

A summary of the varying taxonomic treatments of *Bovicola*, its subgenera and synonyms, is presented in Table 3.

Subgenus **BOVICOLA** Ewing

(Figs 3, 42, 45, 46, 48, 49, 51–54)

- Bovicola* Ewing, 1929: 193. Type-species: *Trichodectes caprae* Gurlt, by original designation.
Bovidoecus Bedford, 1929: 518. Type-species: *Pediculus bovis* Linnaeus, by original designation. [Synonymy by Bedford, 1932a: 356.]
Rhabdopedilon Kéler, 1938a: 453. Type-species: *Trichodectes longicornis* Nitzsch, by original designation. [Synonymy by Werneck, 1950: 59.]

DESCRIPTION. Clypeal marginal carina not broadened medially, or more or less broadened into bar with posterior margin straight or matching curvature of osculum. Temple margin smoothly convex, lacking projection on postero-lateral angle, not convexly produced posteriad to great extent. Male scape not expanded or only slightly expanded. Dorsum of head with setae short or of moderate length, of greater abundance anteriorly than posteriorly. Sitophore sclerite unmodified.

Thorax with lateral and dorsal setae long and of moderate length, sometimes abundant and numerous on disc of prothorax and pterothorax, otherwise less abundant and sparsely scattered on disc of pterothorax with only two setae present on disc of prothorax; setae present along lateral margins and posteriorly (dorsally) on prothorax and pterothorax; posterior setal row of prothorax marginal, with median gap present or absent; posterior setal row of pterothorax submarginal, with median gap absent, row incorporating two very long setae between postero-lateral and postero-median angles or, if setae generally abundant on thorax, postero-lateral setae of pterothorax longer than others.

Abdominal setae short, long or of medium length; setal bases, at least of setae of posterior setal row on sterna and terga, enlarged, clearly with doubled margins. Pregenital sclerites present on sterna and terga (where present) of all segments, except sometimes tergum I and (independently) tergum VIII of males; terga of males, at least of segments IV–VI, with both anterior and posterior sclerites.

Gonapophyses with lobe rectangular, acute, rounded or not pronounced; marginal setae confined to lobe, long. Ventral vulval margin not sclerotised; convex, biconvex with median indentation, or convex with small median membranous projection (Fig. 42); margin smooth or spinose. Postgenital area lacking spinose patch. Genital chamber with antero-median dorsal area lacking spicules, scales or other decoration, either very narrow and strongly-defined or wide and ill-defined, or with very narrow longitudinal fold.

Male subgenital plate variable; sternites VII and IX present, fused to s.g.p.r., sternite VIII absent or, if present, fused or not fused to s.g.p.r. (Figs 46, 48). Pseudostyli absent (Fig. 49) or, if present, setose and lobulate (Figs 46, 48). Basal apodeme very concave anteriorly, the sides of the concavity frequently being parallel, though sometimes obscure. Parameres with broad basal flange or block; sometimes very reduced. Basiparameral sclerites present and fused, or absent. Mesomeres, if fused apically, forming very narrow arch lacking median extension; otherwise mesomeres not fused, sometimes very reduced and obscure. Male genitalia depicted in Figs 51–54.

HOSTS. Bovidae and Cervidae (Artiodactyla).

COMMENTS. Some of the species in this subgenus are parthenogenetic.

SPECIES INCLUDED

- alpinus* Kéler, 1942 (5 ♂, 3 ♀)
bovis (Linnaeus, 1758) (7 ♂, 137 ♀)
caprae (Gurlt, 1843) (c. 50 ♂, c. 50 ♀)
concavifrons (Hopkins, 1960) [Recalled from synonymy with *longicornis* (Nitzsch).] (2 ♂, 98 ♀)
jellisoni Emerson, 1962 (10 ♂, 10 ♀)
limbatus (Gervais, 1844) (c. 50 ♂, c. 65 ♀)
longicornis (Nitzsch, 1818) (44 ♀)
oreamnidis (Hopkins, 1960) (holotype ♂)
ovis (Schränk, 1781) (59 ♂, 64 ♀)
tarandi (Mjöberg, 1910) (2 ♀, 7 nymphs)
tibialis (Piaget, 1880) (c. 100 ♀)

Subgenus **HOLAKARTIKOS** Kéler **gen. rev., stat. n.**

(Figs 44, 47, 57)

Holakartikos Kéler, 1938a: 461. Type-species: *Trichodectes pilosus* Piaget (nec Giebel) [= *Trichodectes crassipes* Rudow], by original designation.

DESCRIPTION. Anterior of head with osculum absent; pulvinus very short, not attaining anterior margin of

head; dorsal preantennal sulcus absent, though ventral preantennal sulcus sometimes present; clypeal marginal carina not always pronounced and not, or only slightly, broadened medially; preantennal portion of head very short, outline smoothly and shallowly rounded. Temple margin smoothly convex, lacking projection on postero-lateral angle, convexly produced posteriad. Male scape very slightly expanded, with setae randomly scattered. Dorsum of head with abundant setae of moderate length; temple with long postero-lateral marginal setae. Sitophore sclerite unmodified.

Thorax with abundant setae, long and of moderate length, present on margins and disc of prothorax and pterothorax; setae longest on the rounded postero-lateral angles of prothorax and pterothorax.

Abdomen with long setae of posterior setal row, and shorter anterior setae, present on sterna, terga and pleura (where present) of all segments (Fig. 47). Pre-genital sclerites sometimes very faint, present on sterna and terga (where present) of all segments except tergum I and sternum II; male terga lacking posterior sclerites.

Gonapophyses with broadly rounded lobe smoothly continuous with ventral margin; marginal setae long, present all along ventral margin, including lobe. Ventral vulval margin not sclerotised; produced into three weakly-developed lobes. Postgenital pleural area with patch of short, spine-like setae. Genital chamber lacking dorsal non-ornamented area or fold.

Male subgenital plate with s.g.p.r. not joining sternites VII and VIII, and sometimes failing to contact either or both; sternites sometimes very faintly sclerotised, obscure; s.g.p.r. with broad lateral flange on VIII and IX (Fig. 47). Pseudostyli absent. Male genital opening dorsal. Basal apodeme long, not concave anteriorly. Parameres long, slender, with basal block and flange. Basiparameral sclerites absent. Mesomeres fused apically, with median extension present (see comments below). Male genitalia depicted in Fig. 57.

HOSTS. Bovidae (Artiodactyla).

COMMENTS. The only included species is not known to be parthenogenetic.

Werneck (1950) failed to recognise the median extension of the mesomeral arch, and considered it absent.

Holakartikos was considered a synonym of *Bovicola* by Werneck (1950) and Emerson & Price (1981); a more extensive history of the variations in status of this subgenus is presented in Table 3.

SPECIES INCLUDED

crassipes (Rudow, 1866) (24 ♂, 31 ♀)

Subgenus **LEPIKENTRON** Kéler gen. rev., stat. n.

(Figs 43, 55)

Lepikentron Kéler, 1938a: 452. Type-species: *Trichodectes breviceps* Rudow, by original designation.

DESCRIPTION. Anterior of head with osculum absent; pulvinus very short, not attaining anterior of margin of head; dorsal preantennal sulcus absent; clypeal marginal carina not pronounced, not broadened medially; preantennal portion of head shorter in male than female, outline broadly and smoothly rounded. Temple margin smoothly convex, lacking projection on postero-lateral angle, not convexly produced posteriad to great extent. Male scape expanded, with setal row apparently present, though setae may be scattered randomly. Dorsum of head with setae of moderate length, slender; setae sparsely distributed, more abundant anteriorly than posteriorly. Sitophore sclerite unmodified.

Thorax with lateral and dorsal setae slender, long and of moderate length; setae present postero-laterally and posteriorly on prothorax and along lateral margins and posteriorly (dorsally) on pterothorax; posterior setal row of prothorax submarginal, sparse, with large median gap; posterior setal row of pterothorax submarginal, with small median gap, setae shorter medially than laterally, with two long setae laterally; pair of setae, widely spaced, present on disc of prothorax dorsally; setae not present on disc of pterothorax.

Abdominal setae of moderate length, slender; anterior setae never present on sterna and terga. Pre-genital sclerites present on terga II–VII (males) and terga III–IX (females) and sterna III–VII (males) and III–VIII (females); male terga III–VII with both anterior and posterior sclerites, though the posterior elements may be very faintly sclerotised and difficult to see.

Gonapophyses with small, pronounced lobe and broad tapering spur (Fig. 43); marginal setae confined to lobe. Ventral vulval margin sclerotised medially; shallowly convex or biconvex (Fig. 43). Postgenital pleural area lacking spinous patch. Genital chamber lacking median non-ornamented area or fold.

Male subgenital plate with sternite VII fused to s.g.p.r. and sternites VIII and IX absent; s.g.p.r. broad. Pseudostyli absent. Male genital opening postero-dorsal. Basal apodeme slightly longer than parameres,

convex anteriorly. Parameres long, slender. Basiparameral sclerites absent. Mesomeres not apically fused; each with median desclerotisation, and appearing as two rods (Fig. 55).

HOSTS. Camelidae (Artiodactyla).

COMMENTS. Only one male of the single included species is known and the species may be parthenogenetic.

The subgenus was treated as a synonym of *Bovicola* by Werneck (1950) and Emerson & Price (1981); a more extensive history of the variations in status of this subgenus is presented in Table 3.

SPECIES INCLUDED

breviceps (Rudow, 1866) (1 ♂, 24 ♀)

Subgenus ***SPINIBOVICOLA*** subgen. n.

(Figs 12, 41, 50, 56)

Type-species: *Trichodectes hemitragei* Cummings.

DESCRIPTION. Anterior of head with osculum absent; pulvinus very short, but attaining anterior margin of head; dorsal preantennal sulcus absent; clypeal marginal carina broadened medially into straight bar with posterior margin slightly irregular; anterolateral margin of head smoothly rounded; preantennal portion short, with outline rounded, almost straight anteriorly. Temple margin convex laterally, straight posteriorly, with short posteriorly-directed projection on postero-lateral angle bearing two setae. Male scape slightly expanded, with setae randomly scattered. Dorsum of head with abundant setae of moderate length. Sitophore sclerite with posterior arms extended (Fig. 12).

Thorax with dorsal and lateral setae abundant, long or of moderate length, present marginally and on disc of prothorax and pterothorax; longest setae present postero-laterally on pterothorax.

Abdomen tapering more acutely in male than in female. Abdomen with posterior setal row comprising long setae on sterna, terga and pleura, anterior setae shorter; anterior setae present on sterna, terga and pleura (where present) of all abdominal segments except sometimes tergum I; male tergum II with curved row of 3–4 long stout setae on each side, modified from posterior setal row, these setae being linked by a curved sclerite (modified tergite) (Fig. 41). Pre-genital sclerites present on terga II–VII or VIII (males) and II–IX (females) and sterna II–VII (males) and II–VIII (females); male terga lacking posterior sclerites.

Gonapophyses with broadly rounded lobe smoothly continuous with ventral margin; marginal setae long, confined to lobe. Ventral vulval margin not sclerotised; convex. Postgenital pleural area lacking spinose patch. Genital chamber lacking dorsal non-ornamented area or fold.

Male segment IX produced posteriorly into narrow, sclerotised extension; subgenital plate tapering characteristically, comprising sternites VI and VII linked by s.g.p.r. (Fig. 50). Pseudostyli absent. Male genital opening dorsal. Basal apodeme not as long as parameres, not concave anteriorly. Parameres fused basally, long and tapering to pointed apices. Basiparameral sclerites absent. Mesomeres absent, or represented by very short sclerites, not apically fused. Male genitalia depicted in Fig. 56.

HOSTS. Bovidae (Artiodactyla).

COMMENTS. Neither of the two included species is known to be parthenogenetic.

SPECIES INCLUDED

hemitragei (Cummings, 1916) (20 ♂, 26 ♀)

multispinosus Emerson & Price, 1979 (8 ♂, 11 ♀)

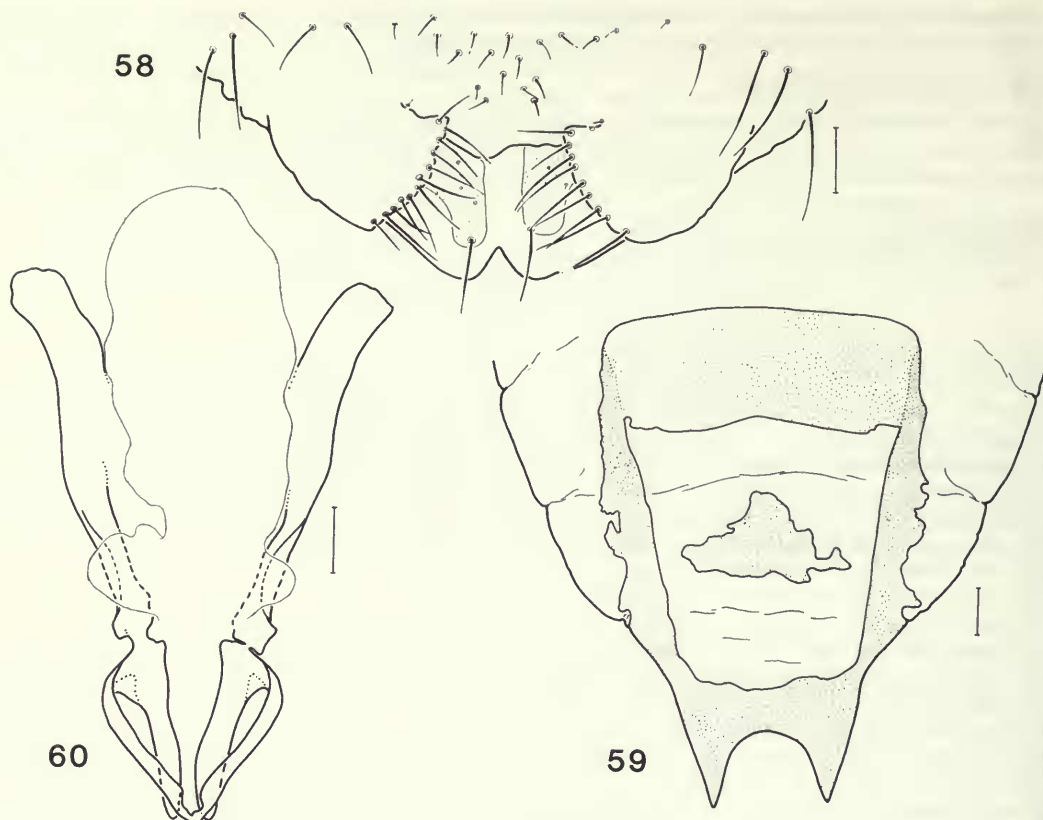
Genus ***BISONICOLA*** gen. n.

(Figs 58–60)

Type-species: *Bovicola sedecimdecembrii* Eichler.

DESCRIPTION. Anterior of head with osculum absent, though pulvinus attaining margin; margin anteriorly to pulvinus membranous, hyaline; dorsal preantennal sulcus present; clypeal marginal carina slightly broadened medially; anterolateral margin of head smoothly convex; preantennal portion of head short or longer, but not as long as postantennal portion, outline broadly rounded, though slightly truncate anteromedially. Temple margin broadly and smoothly convex. Male scape expanded, with setae randomly scattered; flagellomeres fused in males and females; male flagellum with two or three basally-articulated 'teeth'; male flagellum not 'roughened' on interior face. Dorsum of head with numerous setae of medium length. Sitophore sclerite unmodified.

Thorax with lateral and dorsal setae long and of moderate length; setae present along lateral margins and



Figs 58–60 *Bisonicola sedecimdecembrii*. 58, ♀ terminalia, ventral. 59, ♂ subgenital plate, setae omitted. 60, ♂ genitalia.

posteriorly (dorsally) on prothorax and pterothorax; posterior setal row on prothorax marginal, with median gap; posterior setal row of pterothorax submarginal, with median gap absent; pterothorax with posterior setal row incorporating two very long setae between postero-lateral and postero-median angles; pair of setae, widely spaced, present on disc of prothorax dorsally; scattered setae sometimes present posteriorly on disc of pterothorax dorsally. Atria of thoracic spiracles very large.

Abdomen oval. Abdominal spiracles present on segments III–VIII. Abdomen with setae short and of medium length; anterior setae present on sterna, terga and pleura; postero-lateral setae absent. Abdominal pleural projections absent. Sclerites present on sterna, terga and pleura (where present) of all pre-genital abdominal segments except tergum I; male terga V, VI and VII with anterior and posterior sclerites.

Gonapophyses broad, truncate; setae present along postero-median margin; ventral lobe absent (Fig. 58). Gonapophyses meet ventral vulval margin acutely, not linked by sclerotised band. Ventral vulval margin not sclerotised; very short, more or less straight; subgenital lobe absent.

Male subgenital plate with sternites VII and IX fused to s.g.p.r., sternite VIII present but not fused to s.g.p.r.; s.g.p.r. heavily sclerotised, widest on sternum VIII (Fig. 59). Pseudostyli present, large, broadly triangular (Fig. 59). Male genital opening dorsal. Parameres separate, rod-like, fused to mesomeral arch. Basiparameral sclerites absent. Mesomeres fused apically; median extension absent. Male genitalia depicted in Fig. 60.

Hosts. Bovidae (Artiodactyla).

SPECIES INCLUDED

sedecimdecembrii sedecimdecembrii (Eichler, 1946) **comb. n.** from *Bovicola* (5 ♂, 4 ♀)

sedecimdecembrii bison (Blagoveshtchenski, 1967) **comb. n.** from *Bovicola* (2 ♂, 1 ♀)

Genus **WERNECKIELLA** Eichler gen. rev.

(Figs 61, 62)

Werneckiella Eichler, 1940: 160. Type-species: *Trichodectes equi* Denny, by original designation.

DESCRIPTION. Anterior of head with osculum absent; pulvinus not attaining margin; dorsal preantennal sulcus present; clypeal marginal carina slightly broader medially than laterally, or not broadened; anterolateral margin of head smoothly convex; preantennal portion of head not long, outline broadly rounded, sometimes slightly flattened anteriorly. Temple margin convex or rectangular. Male scape expanded, with setae randomly scattered; flagellomeres fused in males and females; male flagellum with two basally-articulated 'teeth'; male flagellum not 'roughened' on interior face. Dorsum of head with abundant short setae. Sitophore sclerite unmodified.

Thorax with lateral and dorsal setae short and of medium length; setae present along lateral margins and posteriorly (dorsally) on prothorax and pterothorax; posterior setal row on prothorax marginal, with median gap; posterior setal row on pterothorax marginal or submarginal, with no median gap; posterior setal row of pterothorax incorporating two very long setae with intervening shorter setae between postero-lateral and postero-median angles; prothorax with seta or setae on disc laterally (dorsally).

Abdomen elongate-oval. Abdominal spiracles present on segments III–VIII. Abdomen with setae short and of moderate length; anterior setae frequently present on sterna and terga, always present on pleura; postero-lateral setae absent. Abdominal pleural projections absent. Sclerites present on abdominal pleura II–VII and sterna and terga of at least abdominal segments II–VII; male terga with single sclerites only.

Gonapophyses broad, truncate, with median faces almost parallel to one another; marginal setae of moderate length; ventral lobe absent. Gonapophyses meet ventral vulval margin acutely, not linked by sclerotised band. Ventral vulval margin not sclerotised, very short, straight; subgenital lobe absent.

Male subgenital plate with sternite VII present and fused to s.g.p.r., sternites VIII and IX absent; s.g.p.r. sinuate and broadest on sternum VIII (Fig. 61). Pseudostyli present, small, simple setose lobes. Male genital opening postero-dorsal. Parameres long, straight or flared and twisted medially, sometimes fused basally. Basiparameral sclerites absent. Mesomeres fused or almost fused into pentagonal mesomeral arch with median extension absent; mesomeres broadest basally (external to b.a.l.s.) and more or less broad distally; mesomeres projecting basally between b.a.l.s. to contact parameres. Male genitalia depicted in Fig. 62.

HOSTS. Equidae (Perissodactyla) and Bovidae (Artiodactyla).

COMMENTS. Some species are parthenogenetic, the males being unknown.

Werneckiella was considered a subgenus of *Damalinia* by Hopkins (1949) and a synonym of *Bovicola* by Werneck (1950); it is here raised from synonymy with *Bovicola*. A more extensive history of the variations in status of this genus is presented in Table 3. The genus was revised by Moreby (1978).

SPECIES INCLUDED

- aspilopyga* (Werneck, 1956) **comb. n.** from *Bovicola* (9 ♂, 11 ♀)
equi (Denny, 1842) **comb. n.** from *Bovicola* (3 ♂, c.100 ♀)
fulva (Emerson & Price, 1979) **comb. n.** from *Bovicola* (4 ♂, ?1 ♀)
neglecta (Kéler, 1942) **comb. n.** from *Bovicola* (5 ♂, 6 ♀)
ocellata (Piaget, 1880) **comb. n.** from *Bovicola* (17 ♀)
zebrae Moreby, 1978 **comb. rev.** from *Bovicola* (1 ♂, 2 ♀)
zuluensis (Werneck, 1950) **comb. n.** from *Bovicola* (13 ♂, 13 ♀)

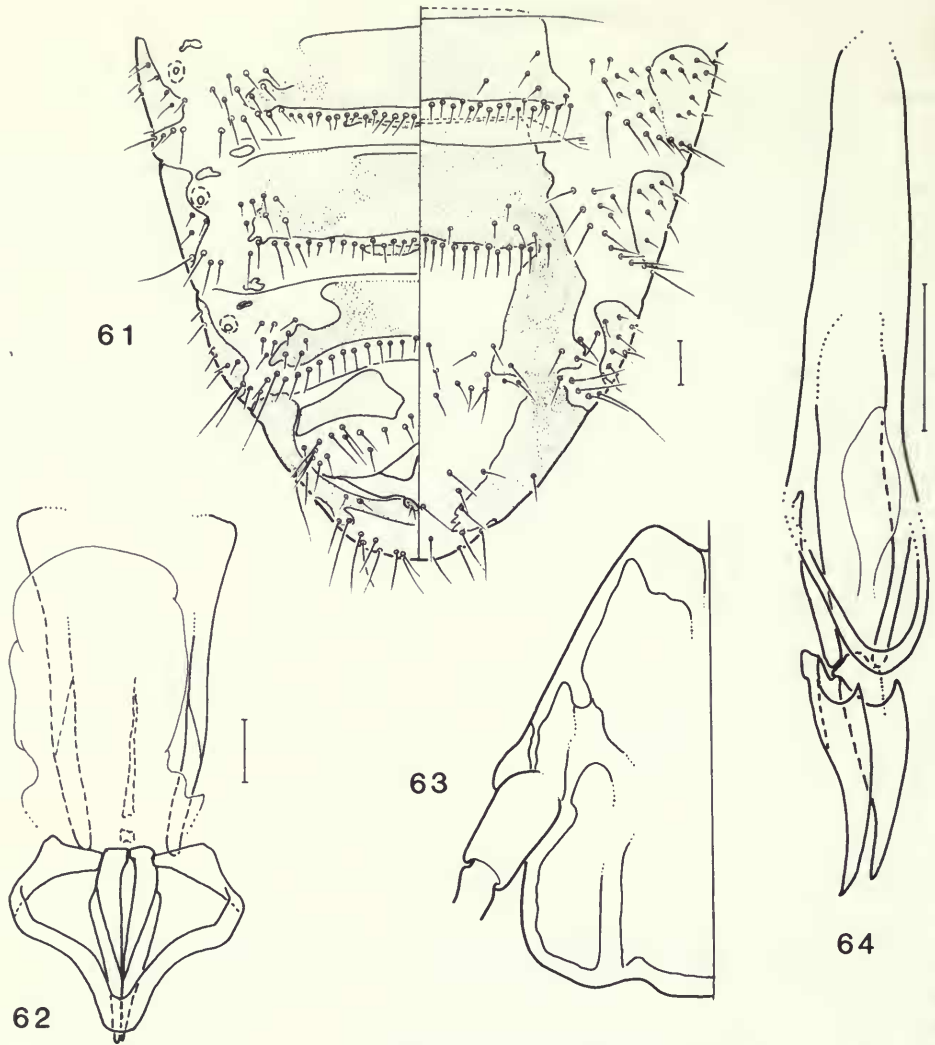
Genus **TRAGULICOLA** gen. n.

(Figs 63, 64)

Type-species: *Damalinia traguli* Werneck.

DESCRIPTION. Anterior of head with osculum present, broad; dorsal preantennal sulcus present; clypeal marginal carina broadened medially into less heavily sclerotised dorsal sclerite, which is broad, posteriorly convex and with median posterior projection (Fig. 63); anterolateral margin of head straight or slightly sinuate; preantennal portion of head as long as its maximum width, outline trapezoid. Temple margin convex or rectangular. Male scape expanded, with setal row present and comprising at least four setae; flagellomeres fused in males and females; male flagellum with two basally-articulated 'teeth'. Dorsum of head with setae short posteriorly and of moderate length anteriorly. Sitophore sclerite unmodified.

Thorax with dorsal setae short or of moderate length; prothorax and pterothorax with marginal or



Figs 61–64 Bovicolinae species. 61, 62, *Werneckiella equi* ♂, (61) terminalia; (62) genitalia. 63, 64, *Tragulicola traguli*, (63) ♀ head, dorsal; (64) ♂ genitalia.

submarginal posterior setal row, the longest setae being posterolaterally except in the male, which has a pair of long setae medially on the posterior row of the pterothorax; male with setal patch centrally on disc of pronotum, but no other setae present on disc of either sex.

Abdomen elongate, with male tapering to more acute posterior angle than female. Abdominal spiracles present on segments III–VIII; atria oblate-spheroids, very large. Abdomen with setae of moderate length, the longest being those comprising the pleural posterior setal row, particularly of the posterior pleura; anterior setae present on all pleura, but not sterna or terga; postero-lateral setae absent. Abdominal pleural projections absent. Sclerites present on sterna, terga and pleura (where present) of all abdominal segments except tergum I, which is reduced and obscure; male terga III–VI with anterior and posterior sclerites.

Gonapophyses broad medially, tapering smoothly distally; ventral margin with long, abundant setae; ventral lobe absent. Gonapophyses meet ventral vulval margin acutely, not linked by sclerotised band. Ventral vulval margin not sclerotised; convex; subgenital lobe absent; marginal spines present, though difficult to see. Female genital chamber with dorsal wall lacking spicules over narrowly triangular area anteromedially.

Male subgenital plate with sternites IX and VIII linked by s.g.p.r., but sternite VII not attached.

Pseudostyli present, short, conical; median ventro-posterior projection also present, longer than pseudostyli. Male genital opening postero-dorsal. Basal apodeme acuminate apically. Parameres broad, triangular, poorly-sclerotised, asymmetrically deflected (may be artifact of preparation, though deflected the same way in all specimens seen). Basiparameral sclerites absent. Mesomeres fused apically, median extension absent; mesomer arch fused to b.a.l.s. about one-third length of basal apodeme anterior from posterior end. Male genitalia depicted in Fig. 64.

HOSTS. Tragulidae (Artiodactyla).

SPECIES INCLUDED

traguli (Werneck, 1950) **comb. n.** from *Damalinia* (70 ♂, 75 ♀)

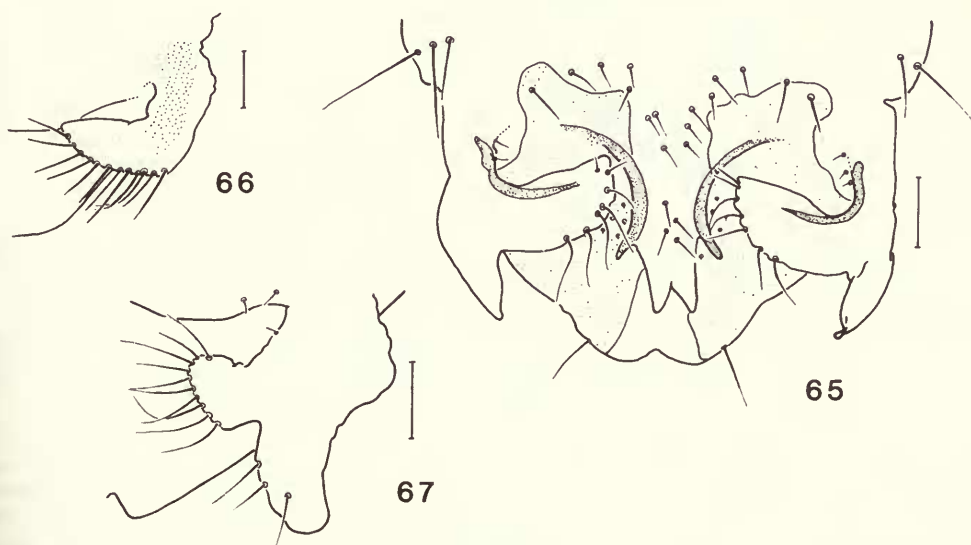
Genus *DAMALINIA* Mjöberg

The genus *Damalinia* comprises three subgenera.

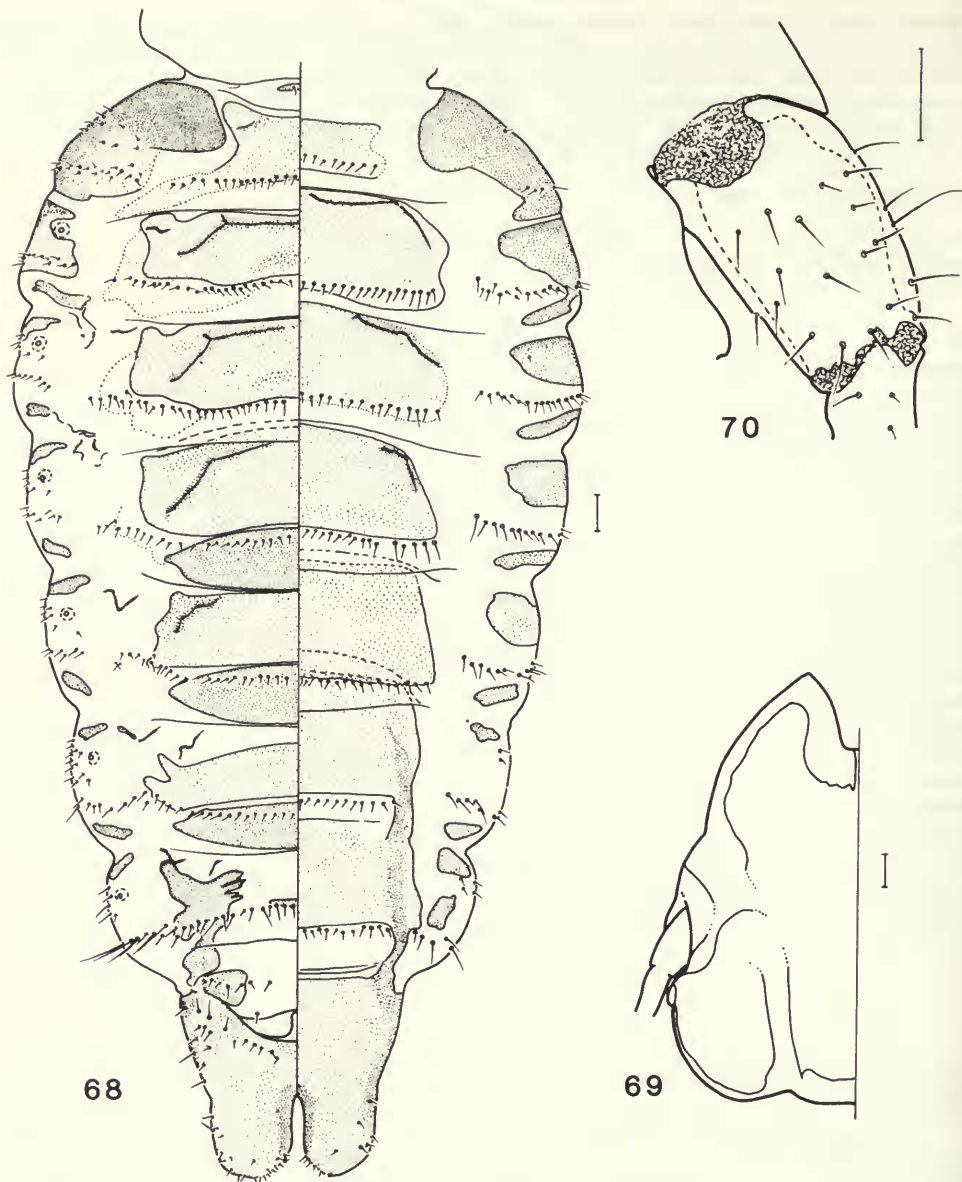
DESCRIPTION. Anterior of head with osculum present, narrow or broad, deep or shallow, or osculum absent, in which case head as described below for *D. (T.) conectens**; dorsal preantennal sulcus present or absent*; clypeal marginal carina more or less broadened medially and of variable form*; anterolateral margin of head straight, slightly concave, slightly sinuate or convex; preantennal portion of head of variable length, outline triangular, trapezoid, rectangular or rounded*. Temple margin smoothly convex, sometimes convexly produced posteriad*, with posterolateral angle sometimes developed laterally or with small posterior rounded projection*. Male scape expanded, with setal row present or setae randomly scattered*; flagellomeres fused in males and females; male flagellum with two or three basally-articulated 'teeth'* and interior face serrate or 'roughened'. Dorsum of head with setae sparse or more or less abundant, short or of moderate length, frequently longer along the anterolateral margins and across the clypeus than elsewhere. Sitophore sclerite unmodified.

Thorax with dorsal and marginal setae short, long or of moderate length, frequently longest on posterolateral margin of pterothorax. Prothorax with setae sparse or absent on anterolateral margin; posterior setal row marginal, though directed onto disc medially and median setal pair sometimes isolated, row more or less sparse, with median gap between setae (other than isolated median pair) present, sometimes wide*; single seta frequently present on dorsal disc anterolaterally. Pterothorax with posterior setal row marginal or submarginal, sometimes irregular or 'doubled*', median gap present or absent, posterior setal row incorporating two very long setae with intervening shorter setae between posterolateral and postero-median angles; setae absent from disc.

Abdomen oval, elongate, or very elongate and narrow*. Abdominal spiracles present on segments III–VIII. Abdominal setae short or of moderate length, frequently longer on pleura than on sterna and



Figs 65–67 *Damalinia* species. 65, *D. (Tricholipeurus) elongata*, ♀ terminalia, ventral. 66, *D. (Cervicola) meyeri*, ♀ gonapophysis, ventral. 67, *D. (C.) hendrickxi*, ♀ gonapophysis, ventral.

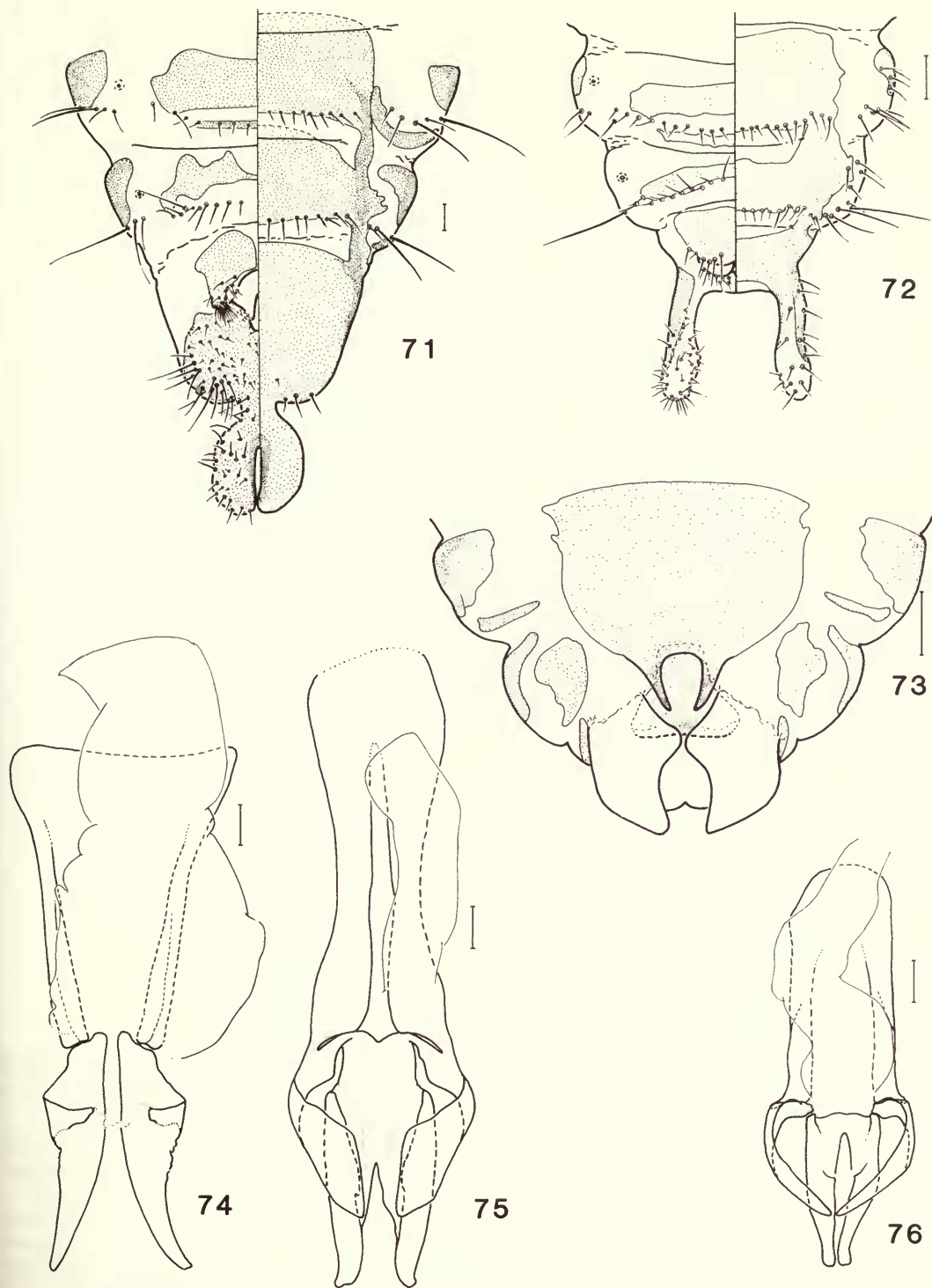


Figs 68–70 *Damalinia* species. 68, *D. (D.) crenelata*, ♂ abdomen. 69, *D. (D.) baxi*, ♀ head, dorsal. 70, *D. (Cervicola) martinaglia*, ♂ scape.

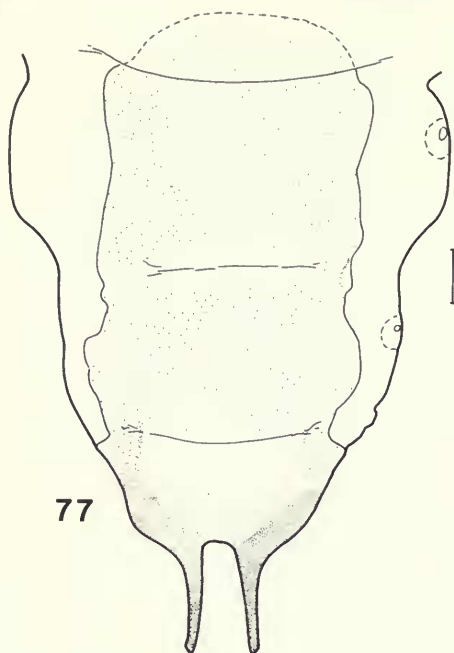
terga; anterior setae present on all pleura except, occasionally, pleurum II, rarely on sterna and terga; postero-lateral setae absent. Abdominal pleural projections absent. Pregenital sclerites present on sterna, terga and pleura (where present) of all segments except tergum I, sometimes absent or very small on pleura (Fig. 80)*; male terga with or without posterior sclerites*.

Gonapophyses variable; ventral margin without rounded lobe, but sometimes with hook-shaped projection*; marginal setae present. Gonapophyses meet ventral vulval margin acutely, not joined by sclerotised band. Ventral vulval margin sclerotised or not sclerotised; subgenital lobe present or absent*. Dorsal margin of vulva and post-vulval area with or without pointed scales*. Common oviduct, at branching point, with or without collar (see subgenus *Cervicola*)*.

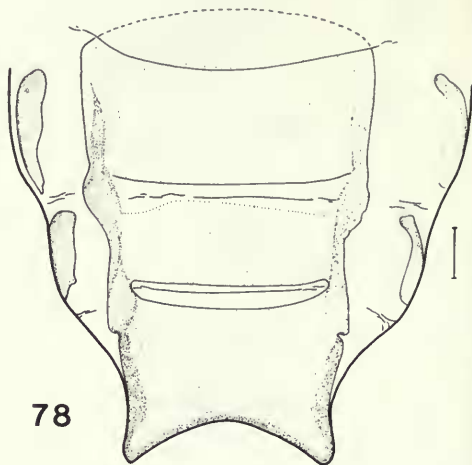
Male subgenital plate variable, sternites VII and VIII always being present and fused to s.g.p.r., sternite IX sometimes modified. Pseudostyli absent or, if present, of variable form*. Posterior margins of tergum



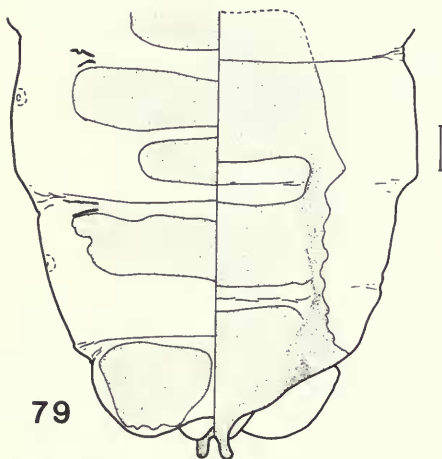
Figs 71–76 *Damalinia* (D.) species. 71, *D. theileri*, ♂ terminalia. 72, *D. appendiculata*, ♂ terminalia. 73, *D. theileri*, ♀ terminalia. 74–76, ♂ genitalia of (74) *D. orientalis*; (75) *D. neotheileri*; (76) *D. crenelata*.



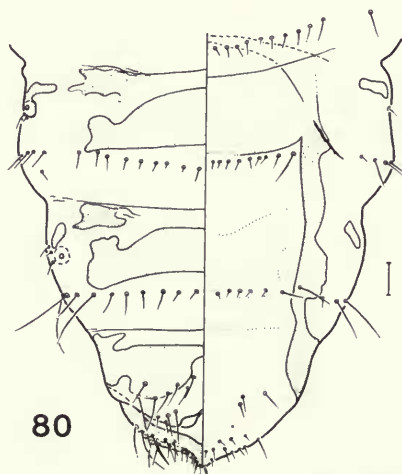
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78



79



80

Figs 77–80 *Damalinia* species, ♂ terminalia. 77, *D. (Cervicola) natalensis*, ventral, setae omitted. 78, *D. (C.) martinaglia*, ventral, setae omitted. 79, *D. (Tricholipeurus) indica*, ventral, setae omitted. 80, *D. (T.) aepycerus*.

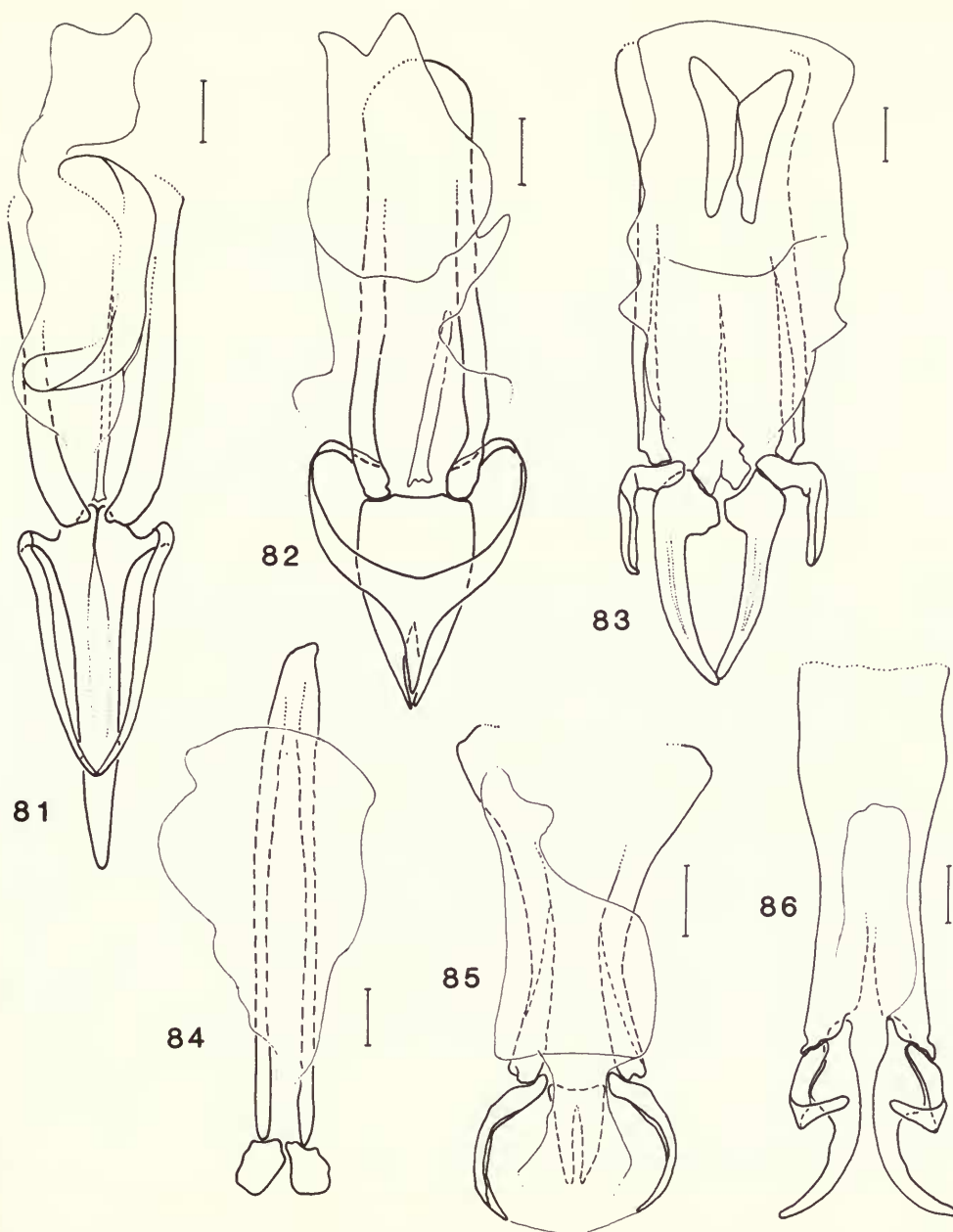
IX sometimes greatly expanded*. Male genital opening postero-dorsal or dorsal. Male genitalia variable*. Hosts. Bovidae and Cervidae (Artiodactyla).

Subgenus **DAMALINIA** Mjöberg

(Figs 11, 68, 71–76)

Damalinia Mjöberg, 1910: 69. Type-species: *Trichodectes crenelatus* Piaget, by monotypy.

DESCRIPTION. Anterior of head with osculum present, narrow or broad, deep or shallow; dorsal preantennal sulcus present; clypeal marginal carina broadened medially either into more or less developed simple



Figs 81–86 *Damalinia* species, ♂ genitalia. 81, *D. (Tricholipeurus) victoriae*. 82, *D. (T.) indica*. 83, *D. (T.) aepycerus*. 84, *D. (Cervicola) hopkinsi*. 85, *D. (C.) meyeri*. 86, *D. (C.) redunca*.

bar with posterior margin straight or concave, or into more or less broad U-shaped sclerite, or into broad, heavily-sclerotised margin of deep osculum; anterolateral margin of head convex or slightly sinuate, in the latter case slightly concave at junction of margin and clypeofrontal sulcus and convex anteriorly; preantennal portion longer or shorter than posterior portion, outline triangular, trapezoid or rounded, sometimes with slight protuberances on either side of osculum. Temple margin smoothly convex, slightly produced posteriad, sometimes with postero-lateral angle developed laterally, or with small posterior rounded projection. Male scape with setae randomly scattered; male flagellum with two basally-articulated 'teeth'. Dorsum of head with setae more or less abundant.

Pterothorax with posterior setal row sometimes irregular or 'doubled'.

Abdomen oval or elongate, sometimes very narrowly elongate. Abdominal setae present anteriorly on all pleura, occasionally on terga and sterna, but only laterally and as irregularity or 'doubling' of posterior setal row. Pleurum II with sclerite extending broadly or narrowly onto sternum II and sometimes tergum II, frequently 'crowding' sternite or tergite II (Fig. 68); pleurites not reduced in size or absent; tergum I lacking sclerite; male terga V and VI (at least) with both anterior and posterior sclerites.

Gonapophyses variable, sometimes hook-shaped, though lacking distal spur, more frequently obtuse, sometimes with ventral (median) margin concave or convex; ventral margin with setae long or of moderate length, abundant, setae sometimes also present on anterior margin. Ventral vulval margin not sclerotised, sometimes short, straight or convex; subgenital lobe absent, though posterior margin of sternum VII sometimes developed into two spikes (Fig. 73). Dorsal margin of vulva and postvulval area usually without pointed scales. Common oviduct without 'collar'.

Male subgenital plate with sternites VII, VIII and IX fused to s.g.p.r., sternite IX and postgenital sclerite sometimes fused; s.g.p.r. more heavily sclerotised than sternites (Fig. 68). Pseudostyli absent or, if present, long and broad, parallel-sided or with basal constriction (Figs 68, 71), or long and narrow (Fig. 72). Posterior margin of tergum IX not greatly expanded. Parameres more or less broad, sometimes fused together. Basiparameral sclerites absent. Mesomeres unfused apically, sometimes fused to b.a.l.s. in characteristic manner (Fig. 75) or to parameres, basally or in entirety, in the latter case apparently absent. Endophallus lacking spicular patch (cf. subgenus *Tricholipeurus*). Male genitalia depicted in Figs 74–76.

Hosts. Bovidae (Artiodactyla).

COMMENTS. Emerson & Price (1982) distinguish their new species *orientalis* (described in *Bovicola*) from the very similar species *thompsoni* Bedford on the following grounds: 'The female of *B. orientalis* is smaller than that of *B. thompsoni* and the lateral margins of the forehead are even [sic] so slightly indented for *B. orientalis* and always even for *B. thompsoni*; the median plates on tergites II–VIII are of different shapes for the two species; the chaetotaxy of terminal abdominal segments is different, with each gonapophysis having at least 20 median and anterior setae for *B. thompsoni* [*orientalis* having, according to the preceding description, 12–17 setae]; and the posterior margin of the temple of *B. thompsoni* has small projections that are not present for *B. orientalis*. The male of *B. thompsoni* is unknown.' Five male and seven female paratypes of *B. orientalis* were examined in this study, together with a further eight males and eight females from the same host (*Capricornis crispus swinhoei*) not examined by Emerson & Price when they prepared their description of *orientalis*, and three females of *thompsoni*, including the holotype. Treating the supposed distinguishing characters in order, the three specimens of *thompsoni* are larger than any of the females from *C. c. swinhoei*; whilst none of the specimens of *thompsoni* has an indentation on the forehead (at the junction of the clypeo-frontal sulcus with the margin), not all of the specimens from *Capricornis c. swinhoei* have either; the shapes of abdominal tergites II–VIII are not significantly different in the two species; the chaetotaxy of the terminal abdominal segments is not different, and no specimen of *thompsoni* has more than 17 setae on the median and anterior margins of the gonapophyses; the small projections of the posterior temple margins are present in all specimens of *orientalis*. It seems, therefore, that the differences between the two species are twofold: host (*orientalis* being described from *Capricornis crispus swinhoei* and *thompsoni* being known only from *Capricornis sumatrensis sumatrensis*), and size. The biological significance of the latter character is not clear, and the two species may be found to differ in other characters not so far discovered. Until a larger sample can be examined, collected from more localities, no taxonomic action is taken to reduce the rank or synonymise *orientalis*, though on the basis of the information so far available the species probably should not stand.

SPECIES INCLUDED

- adenota* (Bedford, 1936) **comb. n.** from *Bovicola* (39 ♂, 35 ♀)
- appendiculata* (Piaget, 1880) (19 ♂, 25 ♀)
- baxi* Hopkins, 1947 (16 ♂, 24 ♀)
- chorleyi* (Hopkins, 1941) (21 ♂, 19 ♀)
- crenelata* (Piaget, 1880) (27 ♂, 20 ♀)
- dimorpha* (Bedford, 1939) **comb. n.** from *Bovicola* (syntype ♀)
- fahrenheitzi* (Eichler, 1949) **comb. n.** from *Tricholipeurus*
- harrisoni* (Cummings, 1916) (3 ♂, 3 ♀)
- hilli* (Bedford, 1934) **comb. n.** from *Bovicola* (42 ♂, 27 ♀)
- neotherleri* Emerson & Price, 1971 (1 ♂, 6 ♀)
- orientalis* (Emerson & Price, 1982) **comb. n.** from *Bovicola* (108 ♂, 135 ♀)
- ornata* Werneck, 1957 (Holotype ♂)
- pelea* (Bedford, 1934) **comb. n.** from *Bovicola*

semitheileri Emerson & Price, 1971 (holotype ♂, allotype ♀)

theileri Bedford, 1928 (2 ♂, 4 ♀)

thompsoni (Bedford, 1936) **comb. n.** from *Bovicola* (3 ♀)

Subgenus **CERVICOLA** Kéler **gen. rev., stat. n.**

(Figs 66, 67, 70, 77, 78, 84–86)

Cervicola Kéler, 1934: 263. [Nomen nudum.]

Cervicola Kéler, 1938a: 460. Type-species: *Trichodectes tibialis* Kéler (nec Piaget) [= *Trichodectes meyeri* Taschenberg], by original designation.

DESCRIPTION. Anterior of head with osculum present, narrow or broad, deep or shallow; dorsal preantennal sulcus present; clypeal marginal carina broadened medially, either into simple bar with posterior margin straight or convex but occasionally with median posterior projection, or into longer posteriorly-developed sclerite with posterolateral angles more or less convex and more or less pronounced median posterior projection; anterolateral margin of head straight or slightly sinuate, in the latter case slightly concave at junction of margin and clypeofrontal sulcus and convex anteriorly; preantennal portion of head as long as or shorter than postantennal portion, outline triangular, trapezoid or rounded. Temple margin smoothly convex, slightly produced posteriorly. Male scape with setae randomly scattered; male flagellum with two basally-articulated 'teeth'. Dorsum of head with setae more or less abundant, sometimes less so posteriorly than anteriorly.

Pterothorax with posterior setal row single.

Abdomen oval or elongate. Abdominal setae present anteriorly on all pleura except, occasionally, pleurum II, but may be very short, fine and difficult to see; anterior setae never on sterna and terga. Pleurum II never with sclerite extending onto sternum II; pleurites not reduced in size or absent; male terga V and VI (at least) with both anterior and posterior sclerites.

Gonapophyses hook-shaped, apex of curved portion acute or rounded, sometimes with distal (dorsal) spur (Figs 66, 67). Gonapophyses with setae long or of moderate length on posterior margin and sometimes on apex of 'hook', smaller setae sometimes present on anterior margin of 'hook'. Ventral vulval margin not sclerotised. Subgenital lobe absent. Dorsal margin of vulva and post-vulval area with pointed scales. Common oviduct at branching-point with folded and more or less apparent 'collar', sometimes partially sclerotised and refracting light when viewed in phase-contrast or bright field transmitted light.

Male subgenital plate with sternites VII, VIII and IX fused to s.g.p.r., though sternite IX sometimes not complete, s.g.p.r. sometimes not attaining posterior margin of segment IX, perisetal gaps sometimes absent; s.g.p.r. more heavily sclerotised than sternites. Pseudostyli absent or, if present, apically pointed and more or less broad (Fig. 78) or apically rounded and very narrow (Fig. 77). Posterior margins of male tergum IX not greatly expanded. Parameres broad or narrow, larger or smaller than mesomeres, may be reduced to small discs, in which case mesomeres absent; parameres fused or unfused; apices sometimes widely divergent. Basiparameral sclerites present or absent. Mesomeres absent or, if present, not fused apically, nor fused to parameres or b.a.l.s. Endophallus lacking spicular patch (cf. subgenus *Tricholipeurus*). Male genitalia depicted in Figs 84–86.

HOSTS. Bovidae and Cervidae (Artiodactyla).

COMMENTS. *Cervicola* was treated as a synonym of *Damalinia* by Werneck (1950), and of both *Damalinia* and *Bovicola* by Hopkins & Clay (1952, pp. 102 and 67 respectively). The history of the variations in status of *Cervicola* is presented in Table 3.

SPECIES INCLUDED

annectens Hopkins, 1943 **comb. rev.** from *Tricholipeurus* (21 ♂, 25 ♀)

forficula (Piaget, 1880) (5 ♂, 8 ♀)

hendrickxi Hopkins, 1947 (4 ♂, 6 ♀)

hopkinsi Bedford, 1936 (15 ♂, 28 ♀)

lerouxii (Bedford, 1930) **comb. n.** from *Tricholipeurus* (9 ♀)

maai Emerson & Price, 1973 (holotype ♂, allotype ♀)

martinaglia (Bedford, 1936) (34 ♂, 27 ♀)

meyeri meyeri (Taschenberg, 1882) (5 ♂, 54 ♀)

meyeri hydropotis (Dobroruka, 1975) **comb. n.** from *Cervicola*

meyeri sika (Dobroruka, 1975) **comb. n.** from *Cervicola*

muntiacus (Séguy, 1948) (12 ♂, 12 ♀)

natalensis Emerson, 1964 (2 ♂, 2 ♀)

reduncae (Bedford, 1929) **stat. n., comb. n.** from *Tricholipecurus* [Raised from subspecies of *D. trabeculae*.] (28 ♂, 29 ♀)

trabeculae (Bedford, 1929) **comb. n.** from *Tricholipecurus* (10 ♂, 10 ♀)

ugandae (Werneck, 1950) **stat. n., comb. n.** from *Tricholipecurus* [Raised from subspecies of *D. trabeculae*.] (14 ♂, 13 ♀)

Unless otherwise stated, all species were previously considered as placed in *Damalinia* s. str.

Subgenus **TRICHOLOIPECURUS** Bedford **stat. n.**

(Figs 4, 7, 8, 13, 65, 79–83)

Tricholipecurus Bedford, 1929: 514. Type-species: *Tricholipecurus aepycerus* Bedford, by original designation.

DESCRIPTION. Anterior of head variable, one of two types.

(a) Osculum absent; pulvinus short, not attaining anterior margin of head; dorsal preantennal sulcus absent; clypeal marginal carina insignificant, not, or only slightly, broadened medially; anterolateral margin of head straight posteriorly, convex anteriorly; preantennal portion of head as long as postantennal portion, outline rounded anteriorly (*D. (T.) conectens* only).

(b) Osculum present, rarely deep; dorsal preantennal sulcus present; clypeal marginal carina broadened medially either into simple bar with posterior margin straight or convex, or into longer posteriorly-developed U- or W-shaped sclerite, with posterolateral angles more or less acutely convex, and frequently with more or less pronounced median posterior projection; anterolateral margin straight, slightly sinuate, or slightly concave; preantennal portion of head longer or shorter than postantennal portion but not short, outline trapezoid or rectangular. Temple margin smoothly convex, more or less convexly produced posteriorly. Male scape with setal row frequently present, comprising four or five setae, though setae sometimes more or less randomly scattered; male flagellum with two or three basally-articulated 'teeth'. Dorsum of head with setae sometimes sparse.

Prothorax with median gap of posterior setal row sometimes almost the width of the posterior margin. Pterothorax with posterior setal row single.

Abdomen usually very elongate, narrow. Abdominal setae present anteriorly on all pleura except, occasionally, pleurum II, but may be very short, fine and difficult to see; anterior setae never on sterna and rarely on terga. Pleurum II never with sclerite extending onto sternum II; pleural sclerites frequently reduced to small anterior plate or absent; tergum I sometimes lacking sclerite; male terga lacking posterior sclerites, or with both anterior and posterior sclerites present on at least segments V and VI (though may be present on any segments up to II–VIII).

Gonapophyses variable, sometimes hook-shaped with distal spur and marginal setae on posterior (dorsal) margin of 'hook', or long with ventral margin convex, straight or sinuate (though not with lobe), apically pointed or rounded; marginal setae of moderate length. Ventral vulval margin sometimes sclerotised; subgenital lobe present, variable, not marginally serrate, ventrally smooth or scaled. Dorsal margin of vulva and post-vulval area without pointed scales. Common oviduct without 'collar'.

Male subgenital plate with sternites VII, VIII and IX fused to s.g.p.r.; perisetal gaps sometimes large, occasionally absent; s.g.p.r. heavily sclerotised and sternites sometimes very lightly sclerotised; s.g.p.r. sometimes curved or sinuate (Fig. 80). Pseudostyli absent or, if present, variable, short and rounded or apically angular, posteriorly or medially directed, narrow or broad, sometimes fused to form single caudal projection. Posterior margins of male tergum IX frequently greatly expanded (Fig. 79). Lateral struts of basal apodeme sometimes with anteposterior spur (Fig. 83). Parameres unfused or, if fused, plate apically pointed or bifurcate. Basiparameral sclerites present or absent. Mesomeres unfused apically or, if fused, symmetric or asymmetric, median extension absent or present; mesomeral arch frequently recurved abruptly at base to contact parameres, sometimes extended between b.a.l.s.; mesomeres not fused to parameres or b.a.l.s. Endophallus with patch of regularly-arranged and numerous spicules sometimes very apparent. Male genitalia depicted in Figs 81–83.

HOSTS. Bovidae and Cervidae (Artiodactyla).

COMMENTS. *Damalinia (T.) longiceps* is included following the statement of Clay & Hopkins (1955) that it resembles *D. (T.) spinifer* Hopkins 'most closely among known species'.

Tricholipecurus has been treated as a genus, synonym (Hopkins, 1943) and subgenus (Hopkins, 1949) of *Damalinia*; the history of the variations in status of *Tricholipecurus* is presented in Table 3.

SPECIES INCLUDED

aepycerus (Bedford, 1929) **comb. n.** from *Tricholipecurus* (1 ♂, 1 ♀)

- albimarginata* (Werneck, 1936) **comb. n.** from *Tricholipeurus* (9 ♂, 13 ♀)
antidorcus (Bedford, 1931) **comb. n.** from *Tricholipeurus* (11 ♂, 18 ♀)
bedfordi (Hill, 1922) **comb. n.** from *Tricholipeurus* (2 ♂, 2 ♀)
clayi (Werneck, 1938) **comb. n.** from *Tricholipeurus* (14 ♂, 12 ♀)
conectens Hopkins, 1943 **comb. rev.** from *Tricholipeurus* (18 ♂, 16 ♀)
cornuta cornuta (Gervais, 1844) **comb. n.** from *Tricholipeurus* (20 ♂, 27 ♀)
cornuta ourebiae Hopkins, 1943 **comb. rev.** from *Tricholipeurus* (18 ♂, 17 ♀)
dorcephali (Werneck, 1936) **comb. n.** from *Tricholipeurus* (2 ♂, 2 ♀)
elongata (Bedford, 1934) **comb. n.** from *Tricholipeurus* (10 ♂, 10 ♀)
indica (Werneck, 1950) **comb. n.** from *Tricholipeurus* (65 ♂, 60 ♀)
lineata (Bedford, 1920) **comb. n.** from *Tricholipeurus* (75 ♂, 83 ♀)
lipeuroides (Megnin, 1884) **comb. n.** from *Tricholipeurus* (106 ♂, 91 ♀)
longiceps (Rudow, 1866)
moschatus (Emerson & Price, 1971) **comb. n.** from *Tricholipeurus* (holotype ♂, disassociated ♂ head)
pakenhami (Werneck, 1947) **comb. n.** from *Tricholipeurus* (21 ♂, 20 ♀)
parallela (Osborn, 1896) **comb. n.** from *Tricholipeurus* (50 ♂, 106 ♀)
parkeri (Hopkins, 1941) **comb. n.** from *Tricholipeurus* (10 ♂, 10 ♀)
spinifer Hopkins, 1943 **comb. rev.** from *Tricholipeurus* (17 ♂, 16 ♀)
victoriae Hopkins, 1943 **comb. rev.** from *Tricholipeurus* (33 ♂, 35 ♀)

EUTRICHOPHILINAE Kéler

Genus *EUTRICHOPHILUS* Mjöberg

(Figs 87–93)

Eutrichophilus Mjöberg, 1910: 71. Type-species: *Eutrichophilus cercolabes* Mjöberg, by subsequent designation (Harrison, 1916a: 21).

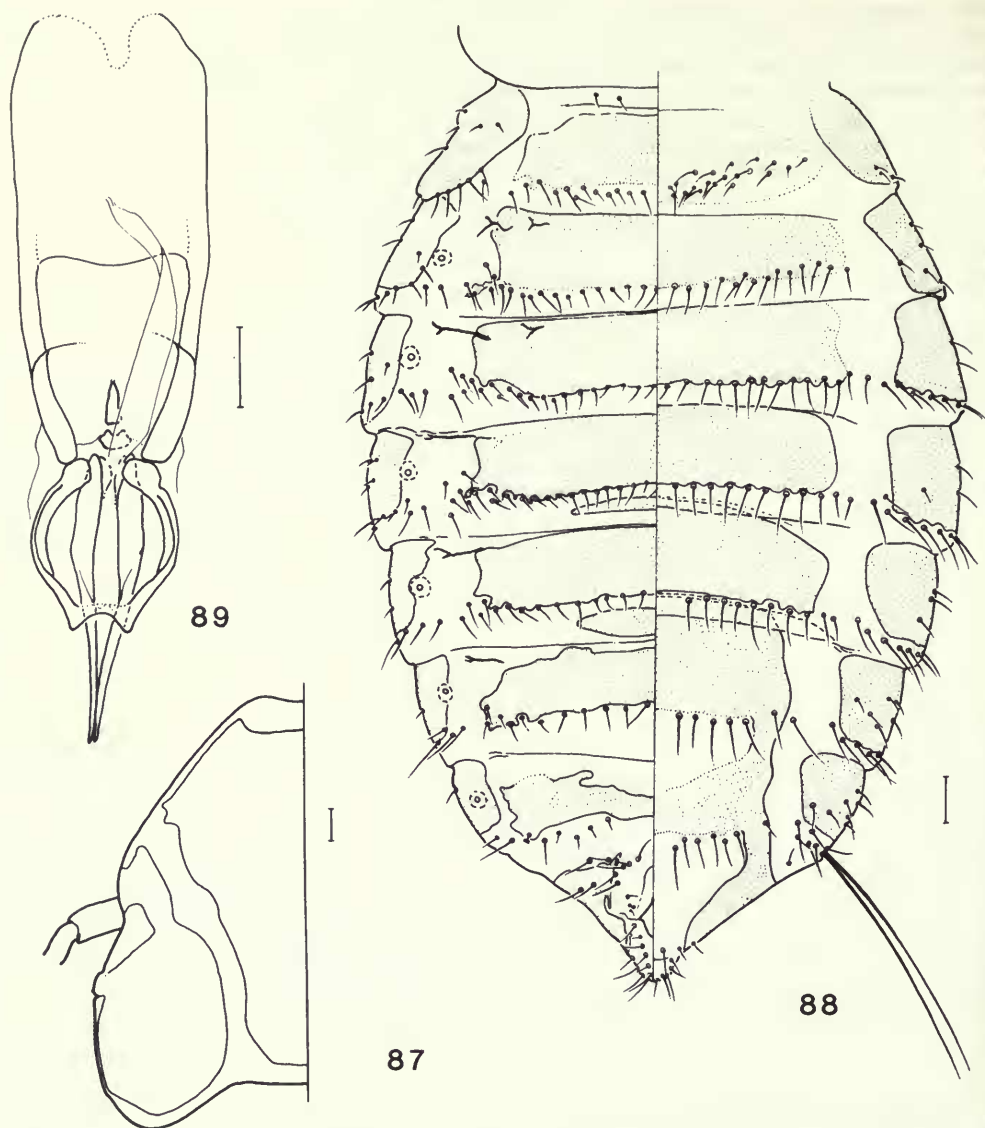
DESCRIPTION. Anterior of head with osculum present or absent, but pulvinus always attaining margin; dorsal preantennal sulcus absent; clypeal marginal carina with median expansion absent or slight, or present as broad or narrow parallel-sided bar with transverse margins convex, straight, or concave; anterolateral margin of head straight or convex; preantennal portion of head long or short; outline triangular, rounded or broadly trapezoid. Temple margin convex or with posterolateral angle apparent; temples greatly expanded posteriorly (Fig. 87). Male scape expanded, with longitudinal setal row present and comprising two setae; male flagellomeres fused; female flagellomeres fused or flagellum comprising two flagellomeres; male flagellum very long, with two basally-articulated 'teeth'. Dorsum of head with setae short or long, sometimes longer anteriorly than posteriorly. Sitophore sclerite unmodified.

Thorax with dorsal setae short or of moderate length marginally or submarginally on posterior of prothorax and pterothorax, absent from disc of both; one or two long setae on posterolateral margins of pterothorax.

Abdomen oval and elongate. Abdominal spiracles present on segments III–VIII. Abdominal setae short or of moderate length, with tufts of long setae on at least pleurum VIII, sometimes also pleurum VII (males) or IX (females) (Fig. 88); anterior setae present on all pleura but absent from sterna and terga; postero-lateral setae present. Abdominal pleura lacking projections dorsally or ventrally. Sclerites present on sterna, terga and pleura (where present) of all pre-genital abdominal segments except, sometimes, tergum I, which may be very small; male terga, at least of abdominal segments V and VI, with anterior and posterior sclerites.

Gonapophyses frequently large, broadly triangular or rounded, ventral margin lacking lobe but with more or less dense marginal setae which are long or of moderate length. Gonapophyses meet ventral vulval margin acutely, not linked by sclerotised band. Ventral vulval margin not sclerotised; smoothly convex, with or without median indentation or setose projection; subgenital lobe absent. Female terminalia depicted in Fig. 90.

Male subgenital plate with sternites VII and VIII present and fused to s.g.p.r., IX absent or, if present, fused to s.g.p.r. (Fig. 88). Pseudostyli absent. Male genital opening dorsal, male segment IX posterior. Parameres long or short, narrow or broad; with basiparameral sclerite or flange sometimes present and fused medially, thus linking parameres, but otherwise unfused. Mesomeres present, fused apically to form arch with no median extension; arch smoothly rounded, or with lateral desclerotisations, in which case median portion is straight and at right angles to lateral portions, very poorly sclerotised and thin, or absent. Male genitalia depicted in Figs 89, 91, 92.

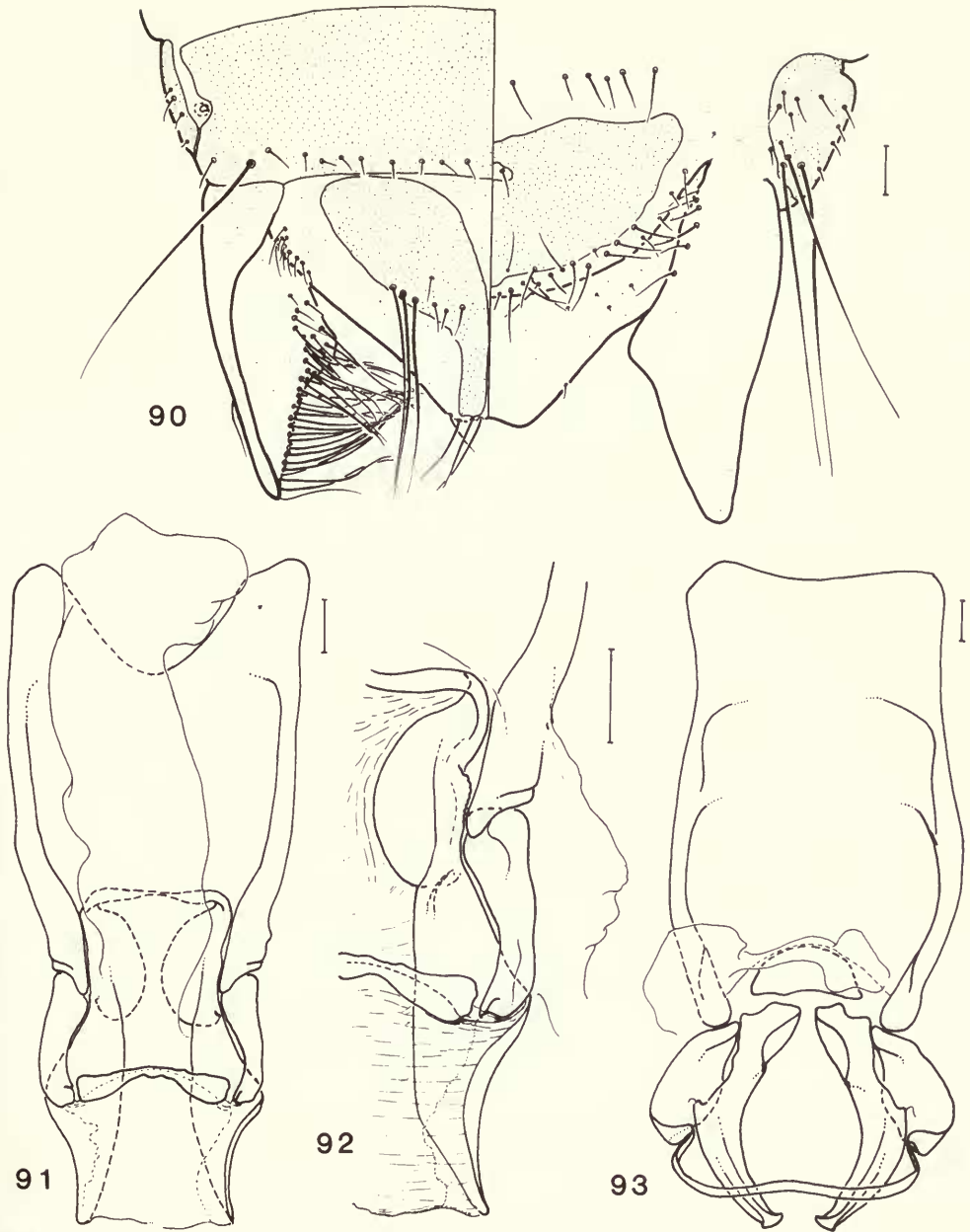


Figs 87–89 *Eutrichophilus* species. 87, *E. minor*, ♀ head, dorsal. 88, *E. setosus*, ♂ abdomen. 89, *E. setosus*, ♂ genitalia.

Hosts. Erethizontidae (Rodentia).

SPECIES INCLUDED

- cercolabes* Mjöberg, 1910 (29 ♂, 25 ♀)
- comitans* Werneck, 1950 (6 ♂, 2 ♀)
- cordiceps* Mjöberg, 1910 (23 ♂, 27 ♀)
- exiguus* Werneck, 1950 (holotype ♂, allotype ♀)
- guyanensis* Werneck, 1950 (8 ♂, 7 ♀)
- lobatus* Ewing, 1936 (5 ♂, 8 ♀)
- maximus* Bedford, 1939 (11 ♂, 11 ♀)
- mexicanus* (Rudow, 1866) (50 ♂, 50 ♀)
- minor* Mjöberg, 1910 (34 ♂, 27 ♀)
- moojeni* Werneck, 1945 (3 ♂, 3 ♀)
- setosus* (Giebel, 1874) (102 ♂, 102 ♀)



Figs 90–93 *Eutrichophilus* species. 90, *E. maximus*, ♀ terminalia. 91, *E. guyanensis*, ♂ genitalia. 92, *E. guyanensis*, ♂ genitalia, detail. 93, *E. moojeni*, ♂ genitalia.

DASYONYGINAE Kéler

Genus *CEBIDICOLA* Bedford

(Figs 94–99)

Cebidicola Bedford, 1936: 52. Type-species: *Trichodectes armatus* Neumann, by original designation.
Meganarion Kéler, 1938a: 465. Type-species: *Trichodectes armatus* Neumann, by original designation.
 [Synonymy by Eichler, 1941.]

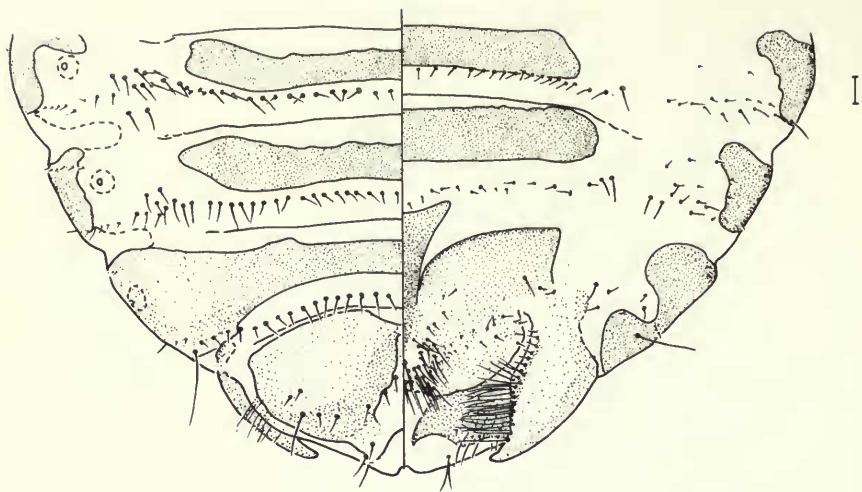


Fig. 94 *Cebidicola armatus*, ♀ terminalia.

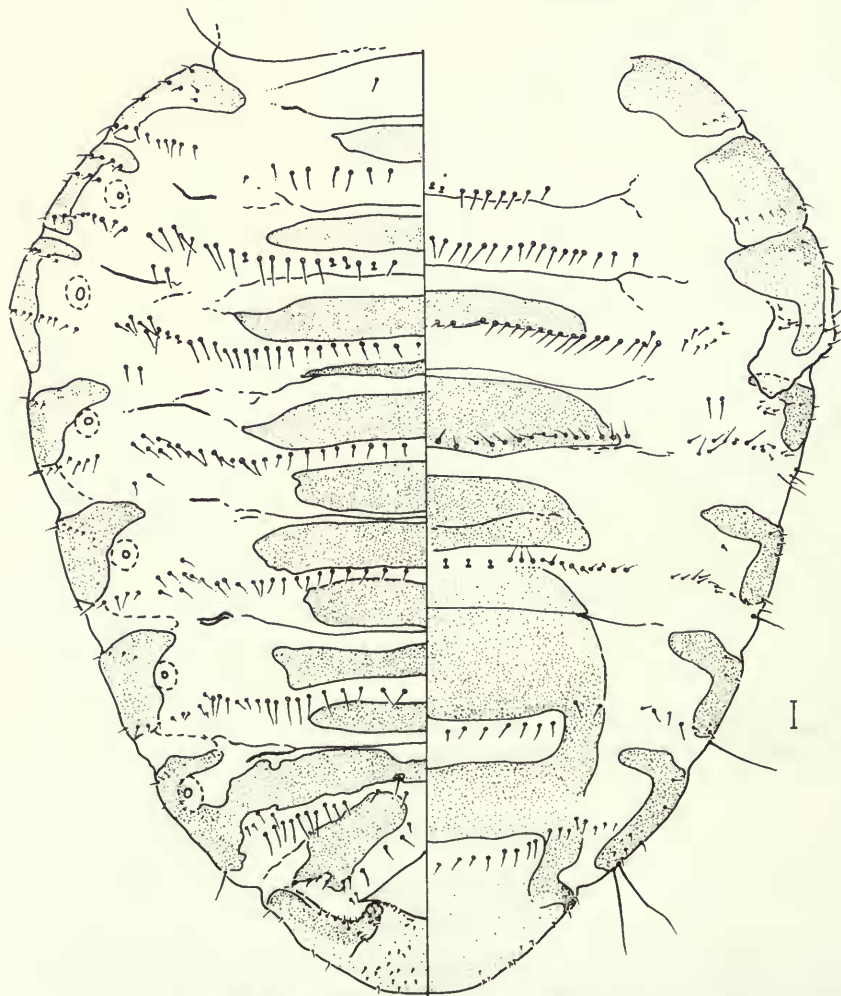
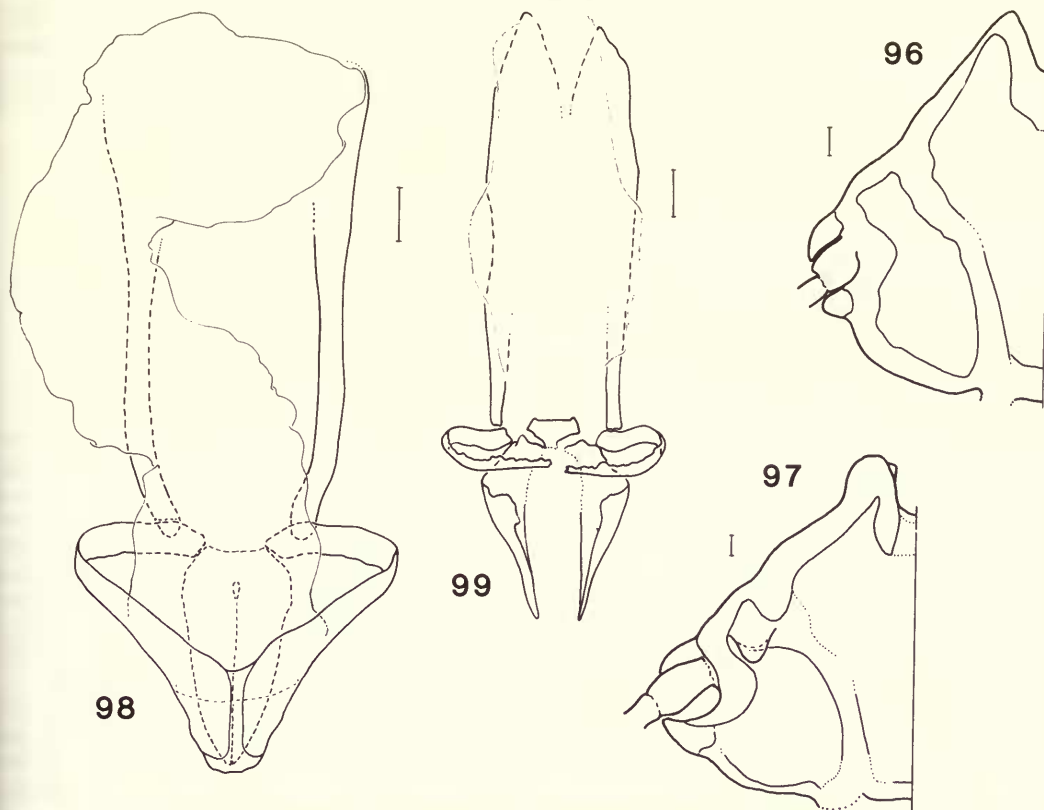


Fig. 95 *Cebidicola armatus*, ♂ abdomen.



Figs 96–99 *Cebidicola* species. 96, *C. semistriatus*, ♀ head, dorsal. 97, *C. armatus*, ♀ head, dorsal. 98, *C. armatus*, ♂ genitalia. 99, *C. extrarius*, ♂ genitalia.

DESCRIPTION. Anterior of head with oculus present, deep; dorsal preantennal sulcus present or absent; clypeal marginal carina broadened medially into dorsal, posteriorly convex, sclerite; anterolateral margin straight, slightly convex, concave or sinuate anteriorly, more or less abruptly concave at junction with clypeofrontal sulcus, with or without anterior sclerotised projection on either side of oculus (Figs 96, 97); preantennal outline broadly triangular. Temple margin convex or slightly acute and angular posterolaterally, with eyes more or less prominent (Figs 96, 97). Male scape expanded, with setal row present and comprising two or more setae; male flagellomeres fused, with two basally-articulated 'teeth'; female flagellomeres fused or unfused. Dorsum of head with setae short or of moderate length, sparse. Sitophore sclerite unmodified.

Tarsal claws lacking ventral spines or teeth. Postcoxae absent or present, not greatly developed. Thoracic setae present dorsally only along posterior and posterolateral margins of pterothorax; setae short medially, longer laterally. Atrium of thoracic spiracle tubular or conical.

Abdomen oval, sometimes tapering posteriorly more in male than female. Abdominal spiracles present on segments III–VIII. Abdominal setae short or of moderate length, longest on pleura VI–VIII; anterior setae sometimes present on pleura and laterally on sterna and terga; postero-lateral setae present, sometimes numbering more than one per site. Pleural projection present ventrally on abdominal pleurum IV, large, sclerotised. Sclerites present on all abdominal pleura, on at least abdominal terga II to VIII and at least abdominal sterna V to VII; male terga, at least on segments V–VII, with anterior and posterior sclerites (Fig. 95).

Gonapophyses broad, especially medially, though lobe absent; marginal setae long, densely crowded. Gonapophyses meet ventral vulval margin acutely, not linked by sclerotised band. Ventral vulval margin not sclerotised; sometimes expanded, otherwise smoothly convex (Fig. 94); bilobed median spinose projection may be present, but subgenital lobe absent. Median longitudinal sclerite sometimes present on female sternum VIII (Fig. 94).

Male subgenital plate with sternite VII fused to s.g.p.r., VIII fused or not fused to s.g.p.r., and IX absent

or, if present, not fused to s.g.p.r. Pseudostyli absent or, if present, small, slender, incurved (Fig. 95). Male genital opening postero-dorsal or dorsal. Parameres fused or unfused; basiparameral sclerites present, fused. Mesomeres present, fused or unfused and, if fused, median extension absent; mesomeral arch produced basally between b.a.l.s. to contact parameres, which do not meet b.a.l.s. Male genitalia depicted in Figs 98, 99.

Hosts. Cebidae (Primates).

SPECIES INCLUDED

armatus (Neumann, 1913) (3 ♂, 4 ♀)

extrarius Werneck, 1950 (21 ♂, 13 ♀)

semiarmatus (Neumann, 1913) (12 ♂, 12 ♀)

Genus *PROCAVICOLA* Bedford

The genus *Procavicola* comprises two subgenera.

DESCRIPTION. Anterior of head with osculum present, semicircular; dorsal preantennal sulcus present; clypeal marginal carina broadened medially into dorsal, posteriorly convex, sclerite (Fig. 106); conus large, as long as female scape; anterolateral margin of head straight or convex anteriorly, more or less abruptly concave at junction with clypeofrontal sulcus; preantennal outline broadly triangular. Temple margin smoothly convex, sometimes produced posteriad, or with postero-lateral angle developed into posteriorly-projecting triangular or rounded process*. Male scape expanded, with setal row represented by two setae only; male flagellomeres fused, with two basally-articulated 'teeth'; female flagellomeres unfused and closely associated, fused to two closely associated annulations, or completely fused*. Dorsum of head with setae short, sparse; anterior margin of head with setae longer than on disc. Sitophore sclerite unmodified.

Tarsal claws lacking ventral spines or teeth. Postcoxae of metathoracic leg absent or present; if present, may be well developed, but not to the same degree as described for *Procaviphilus* (*Meganarionoides*) and not fused to abdominal pleurite II. Thoracic setae present dorsally only along posterior and latero-posterior margins of prothorax and pterothorax; setae short, except for laterally on pterothorax, where of moderate length.

Abdomen oval, more or less elongate (Figs 103, 105). Abdominal spiracles present on segments III–VIII, all approximately the same size. Abdominal setae short or of moderate length; anterior setae present on pleura only; postero-lateral setae present, sometimes numbering more than one per site*. Pleural projections present dorsally and ventrally on abdominal pleurum IV, sclerotised. Sclerites present on sterna, terga and pleura of all abdominal segments except, occasionally, tergum I*; male terga, at least of segments IV–VI, with anterior and posterior sclerites; second abdominal sternum with broad, heavily-sclerotised apophysis underlying sternite, articulating with median extensions of abdominal pleurite II (Figs 103, 105).

Gonapophyses broad, lacking lobe; marginal setae lacking tubercles, occasionally on small conical protuberances (Figs 101, 102). Gonapophyses meet ventral vulval margin acutely, not linked by sclerotised band. Ventral vulval margin not sclerotised; expanded, sometimes W-shaped medially (Fig. 100), sometimes broadened posteriorly (Fig. 101), sometimes contracted, shorter than length of gonapophyses (Fig. 102)*.

Male subgenital plate with sternites VII and VIII present and fused to s.g.p.r., sternite IX absent or, if present, fused to s.g.p.r. and perisetal gaps small*; s.g.p.r. not always attaining posterior margin of segment IX*. Pseudostyli absent (Figs 103–105). Male genital opening postero-dorsal. Male genitalia very variable*; parameres not fused, basiparameral sclerites present or absent*, mesomeres fused or unfused*.

Hosts. Procaviidae (Hyracoidea).

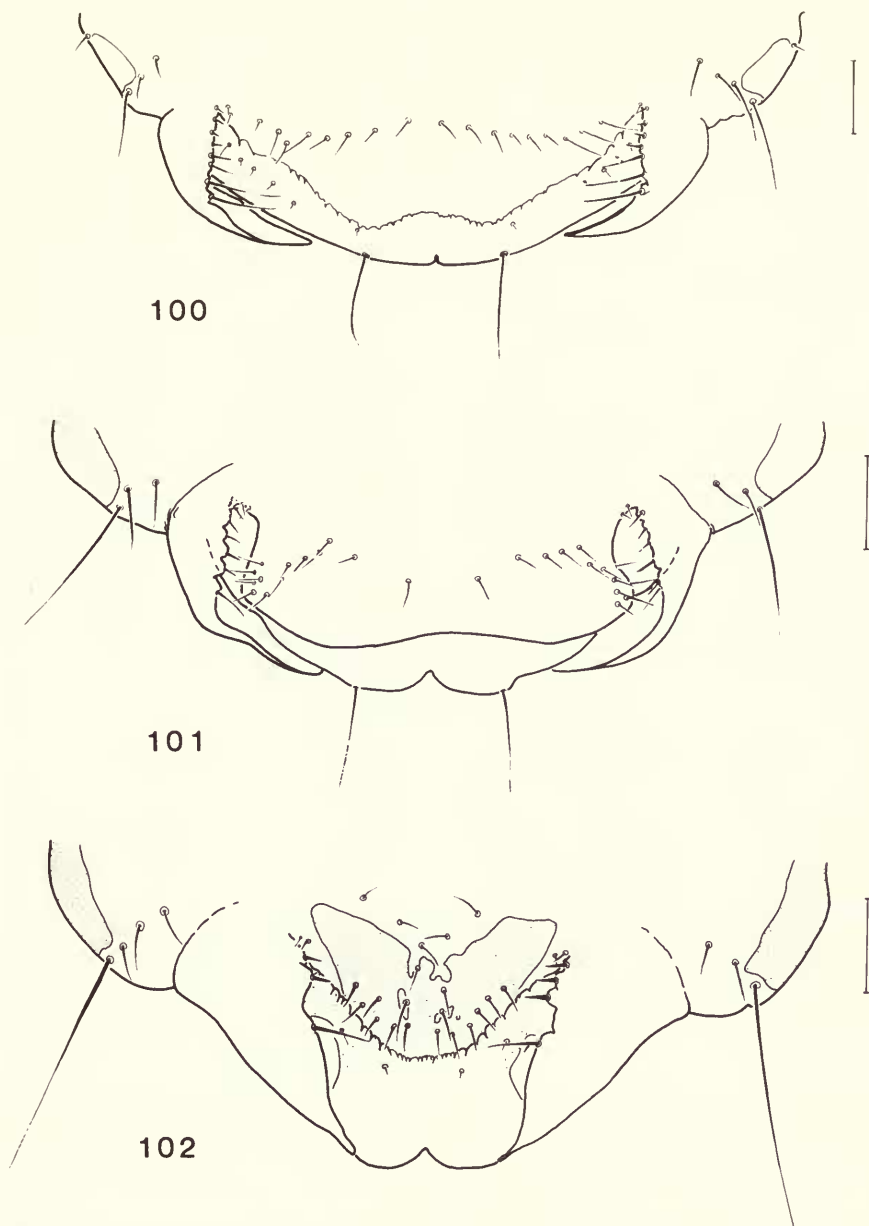
Subgenus *PROCAVICOLA* Bedford

(Figs 100, 104–106, 109)

Procavicola Bedford, 1932: 711. Type-species: *Trichodectes sternatus* Bedford, by original designation.

DESCRIPTION. Temple margin smoothly convex, sometimes projecting posteriorly, but never with posterior membranous or lightly-sclerotised process.

Postero-lateral setae present, single at each site. Sclerites present on sterna, terga and pleura of all abdominal segments except segment I, where tergal sclerite absent.



Figs 100–102 *Procavicola* species, ♀ terminalia, ventral. 100, *P. (P.) natalensis*. 101, *P. (Condylocephalus) lindfieldi*. 102, *P. (C.) dissimilis*.

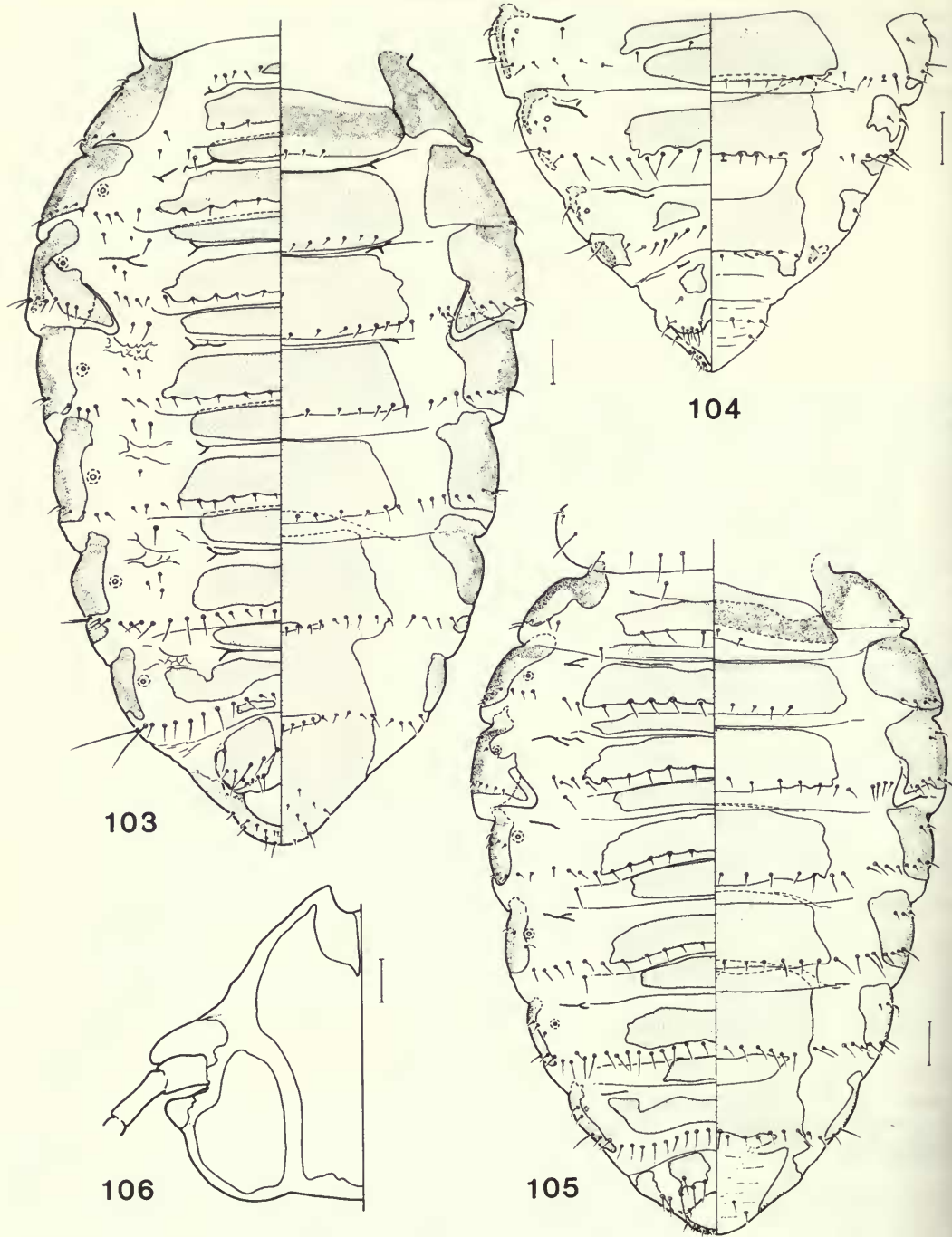
Ventral vulval margin expanded as described, much broader than length of gonapophyses (Fig. 100).

Male subgenital plate with sternites VII and VIII present and fused to s.g.p.r., sternite IX absent; s.g.p.r. may be very slender, may not attain posterior margin of segment IX (Figs 104, 105). Parameres unfused, more or less narrow, rod-like, sometimes asymmetrically curved. Basiparameral sclerites frequently present, fused or separate. Mesomeres not fused, short. Endophallus lacking large, hook-like sclerites. Male genitalia depicted in Fig. 109.

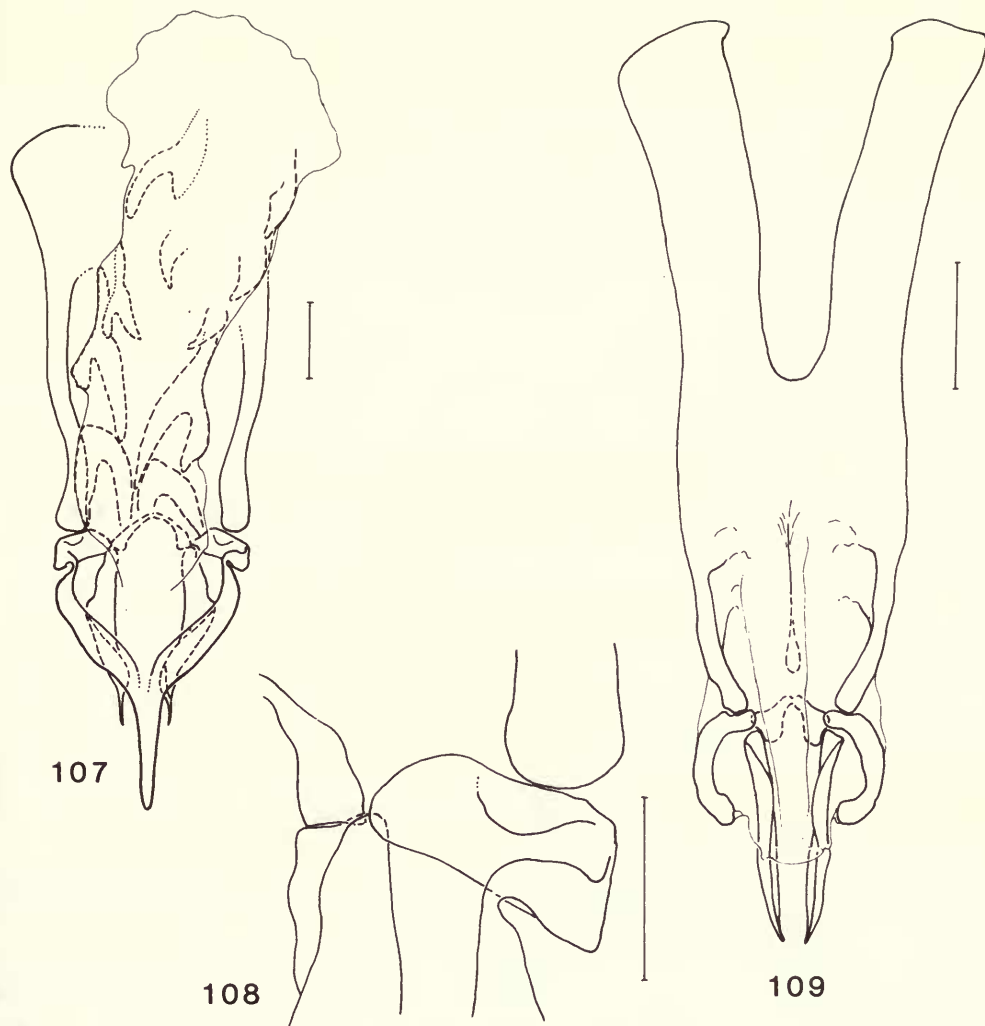
HOSTS. Procaviidae (Hyracoidea).

SPECIES INCLUDED

affinis Werneck, 1941 (10 ♂, 13 ♀)



Figs 103–106 *Procavicola* species. 103, *P. (Condylocephalus) dissimilis*, ♂ abdomen. 104, *P. (P.) vicinus*, ♂ terminalia. 105, *P. (P.) eichleri*, ♂ abdomen. 106, *P. (P.) natalensis*, ♀ head, dorsal.



Figs 107–109 *Procavicola* species, ♂ genitalia. 107, *P. (Condylocephalus) dissimilis*. 108, *P. (C.) dissimilis*, detail of right paramere and mesomere at junction with basal apodeme. 109, *P. (P.) pretoriensis*.

- brucei* Werneck, 1941 (43 ♂, 48 ♀)
eichleri Werneck, 1941 (45 ♂, 56 ♀)
emarginatus (Bedford, 1928) (16 ♂, 19 ♀)
furca Bedford, 1939 (1 ♂)
heterohyracis Bedford, 1932 (3 ♂, 1 ♀)
lopesi lopesi Bedford, 1939 (32 ♂, 40 ♀)
lopesi vicinus Werneck, 1941 (8 ♂, 10 ♀)
mokeetsi Bedford, 1939 (20 ♂, 15 ♀)
natalensis Bedford, 1932 (23 ♂, 12 ♀)
parvus Bedford, 1932 (8 ♂, 6 ♀)
pretoriensis Bedford, 1932 (23 ♂, 21 ♀)
shoanus Maltbaek, 1937
sternatus (Bedford, 1928) (9 ♂, 8 ♀)
subparvus Bedford, 1932 (6 ♂, 9 ♀)
thorntoni Hopkins, 1942 (18 ♂, 22 ♀)
ugandensis Werneck, 1941 (17 ♂, 18 ♀)

Subgenus **CONDYLOCEPHALUS** Werneck

(Figs 101–103, 107, 108)

Condylocephalus Werneck, 1941: 497 [as subgenus of *Procavicola* Bedford]. Type-species: *Procavicola (Condylocephalus) bedfordi* Werneck, by original designation.

DESCRIPTION. Temple margin convex, with posteriorly-projecting membranous or lightly-sclerotised process, more apparent in male than female, triangular or as small rounded bump (*linfieldi* females). Female flagellomeres unfused, but closely associated.

Abdomen with postero-lateral setae present, frequently doubled, trebled or numerous at each site. Sclerites present on sterna, terga and pleura of all abdominal segments.

Ventral vulval margin expanded, sometimes broadened posteriorly and broader than length of gonapophyses (Fig. 101), otherwise narrower, width less than length of gonapophyses (Fig. 102).

Male subgenital plate with sternites VII, VIII and IX present and fused to s.g.p.r., with perisetal gaps small (Fig. 103). Parameres unfused, curved, with anterolateral projections, not asymmetric. Basiparameral sclerites present, fused or unfused. Mesomeres fused apically; mesomeral arch with median extension and lateral double flexion (Figs 107, 108). Endophallus ornamented with large, hook-like sclerites (Fig. 107).

HOSTS. Procaviidae (Hyracoidea).

COMMENTS. Though *Condylocephalus* has been treated by most authors as a subgenus of *Procavicola*, Eichler (1963) considered it to have full generic status.

SPECIES INCLUDED

bedfordi Werneck, 1941 (2 ♂, 1 ♀)

dissimilis Werneck, 1941 (64 ♂, 58 ♀)

hopkinsi Werneck, 1941 (24 ♂, 29 ♀)

linfieldi (Hill, 1922) (77 ♂, 65 ♀)

univirgatus (Neumann, 1913) (33 ♂, 32 ♀)

Genus PROCAVIPHILUS Bedford

The genus *Procaviphilus* comprises two subgenera.

DESCRIPTION. Surface of head, thorax and abdomen frequently covered with clearly-visible scales or sclerotised nodules.

Anterior of head variable, one of two types: 'procaviphilus' or 'procavicola'*.

(a) 'procaviphilus' type. Osculum absent or, if present, slightly concave only; dorsal preantennal sulcus absent; clypeal marginal carina broadened medially into straight or slightly curved bar (Fig. 112); conus small, not as long as female scape; anterolateral margin of head straight or convex anteriorly, no abrupt concavity at junction with clypeofrontal sulcus; preantennal outline trapezoid (Fig. 112).

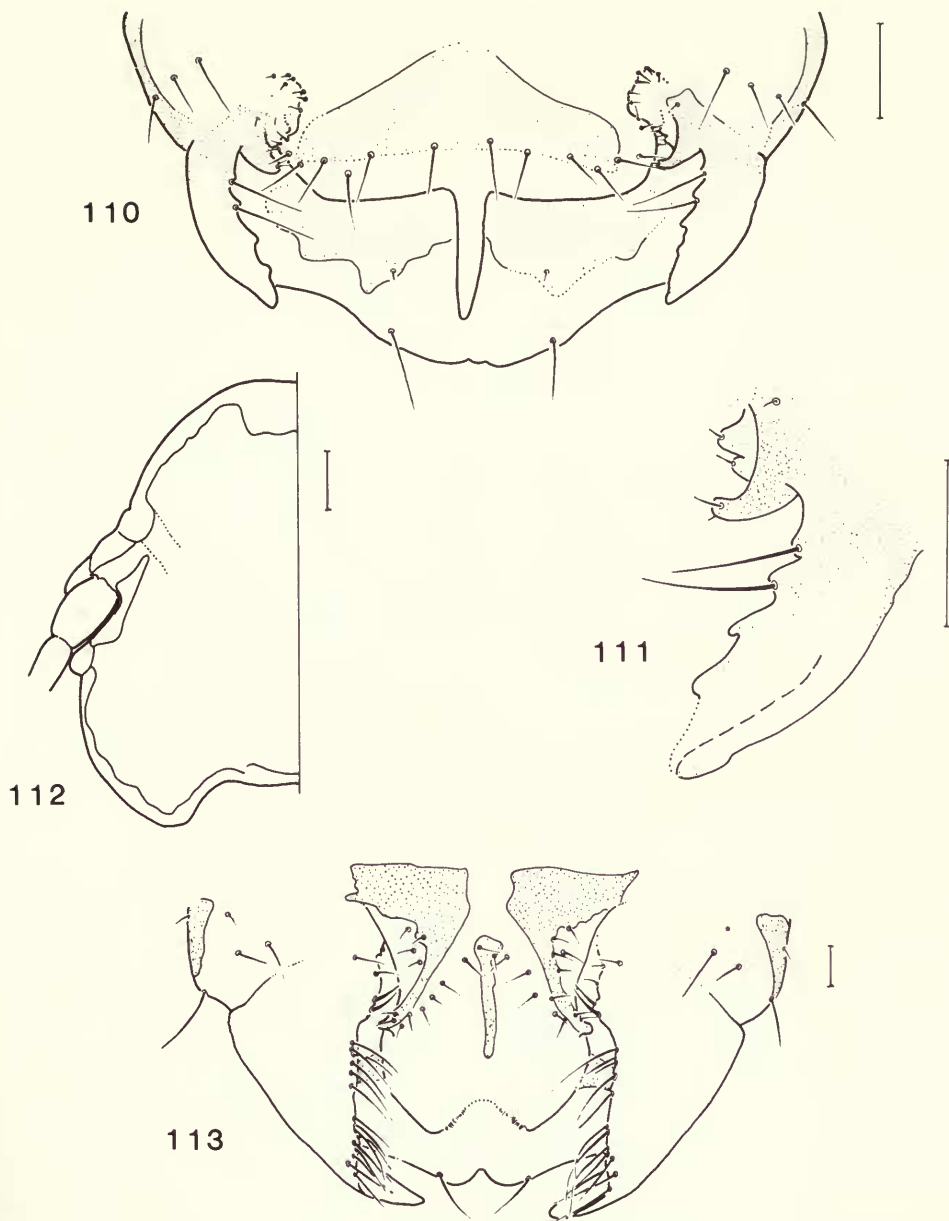
(b) 'procavicola' type. Osculum present, semicircular; dorsal preantennal sulcus present or absent; clypeal marginal carina broadened medially into dorsal, posteriorly convex, sclerite (Fig. 106); conus large, as long as female scape; anterolateral margin of head convex anteriorly, more or less abruptly concave at junction with clypeofrontal sulcus; preantennal outline broadly triangular.

Temple margin smoothly convex, more or less projecting posteriorly. Male scape expanded, with setal row represented by two setae only; male flagellomeres fused, with two basally-articulated 'teeth'; female flagellomeres unfused, though sometimes very closely associated. Dorsum of head with setae short, sparse. Sitophore sclerite unmodified.

Tarsal claws lacking ventral spines or teeth. Postcoxale of leg III absent or, if present, frequently enlarged, heavily sclerotised, displaced posteriad to occupy abdominal sternum II, and fused to sclerite of abdominal pleurum II, in which case gap between postcoxae sometimes obscured by sternite II*. Thoracic setae present dorsally only along posterior and lateroposterior margins of prothorax and pterothorax; setae short, except for laterally on pterothorax, where of moderate length.

Abdomen oval-elongate. Abdominal spiracles present on segments III to VIII, though sometimes very small and possibly non-functional on VIII*. Abdominal setae short or of moderate length; anterior setae present on pleura only, sparse; postero-lateral seta present. Pleural projections present ventrally and dorsally on abdominal pleurum IV, sclerotised. Sclerites, frequently faint, present on sterna, terga and pleura of all abdominal segments except I; male terga, especially tergum VI, frequently with anterior and posterior sclerites.

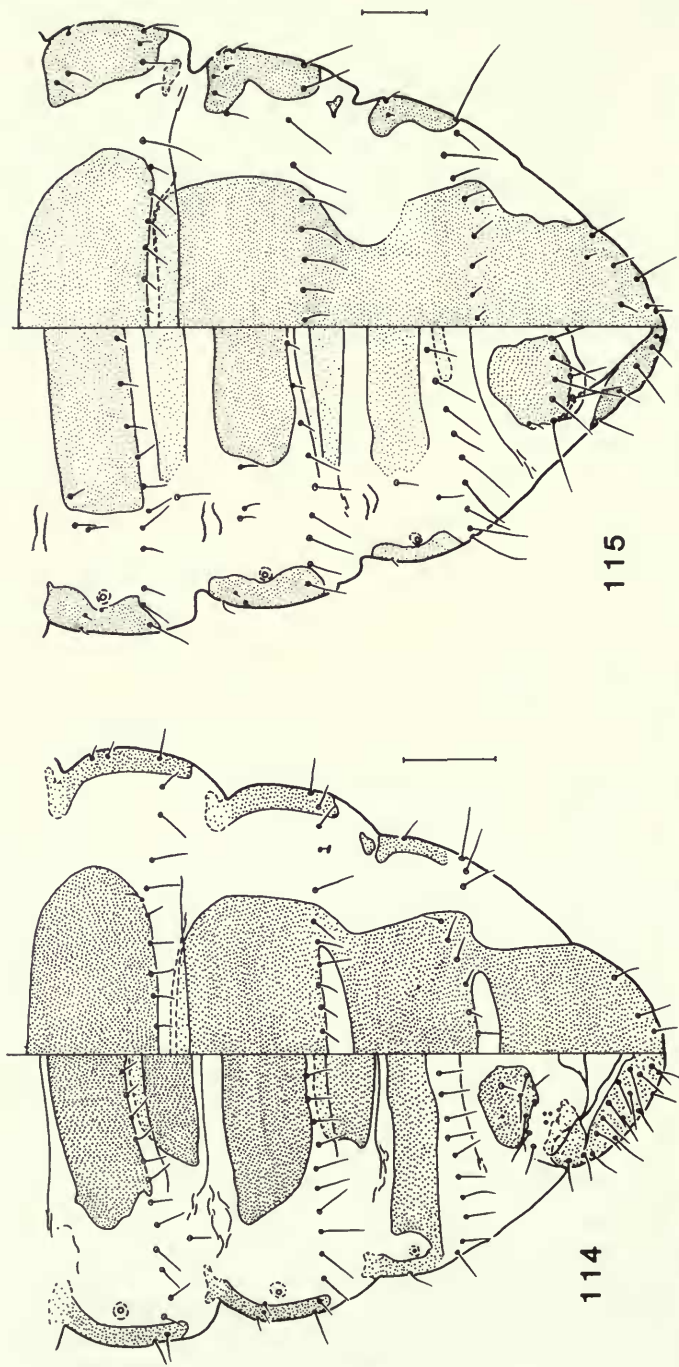
Gonapophyses with setae non-tuberculate and, frequently, tuberculate; setal tubercles, if present,



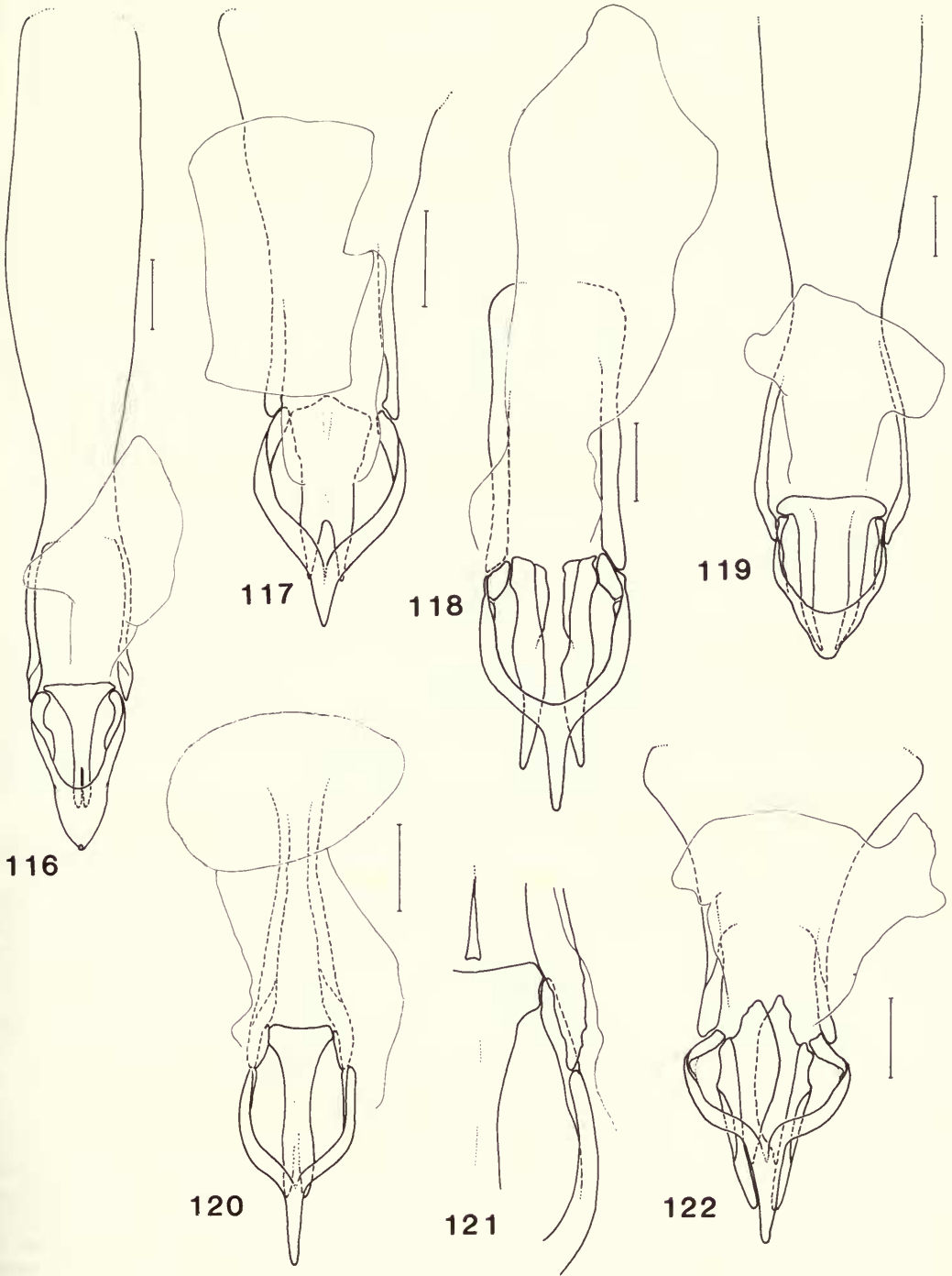
Figs 110–113 *Procaiviphus* species. 110, *P. (Meganarionoides) n. baculatus*, ♀ terminalia, ventral. 111, *P. (M.) n. baculatus*, ♀ gonapophysis, ventral. 112, *P. (P.) f. granuloides*, ♀ head, dorsal. 113, *P. (M.) scutifer*, ♀ terminalia, ventral.

sometimes fused characteristically*; lobe absent or, if apparently present, formed of fused tubercles and thick, with submarginal setae (Fig. 111). Gonapophyses meet ventral vulval margin acutely, not linked by sclerotised band. Ventral vulval margin not sclerotised; expanded, frequently with posterior broadening (Fig. 110), sometimes lengthened (Fig. 113) or with median lobulate process (Fig. 110)*.

Male subgenital plate with sternites VII, VIII and IX present and fused to s.g.p.r., perisetal gaps very small or absent, rarely large (Figs 114, 115). Pseudostyli absent. Male genital opening posterodorsal. Male genitalia very variable: basal apodeme short or long with median constriction*; parameres unfused, frequently with basal flange, or fused, faintly or clearly, and parameral plate apically bifurcate. Basiparameral sclerites absent. Mesomeres fused, basally extending between b.a.l.s. to contact parameres, which



Figs 114, 115 *Procaviphilus* (*Meganarionoides*) species, ♂ terminalia. 114, *P. (M.) angolensis*. 115, *P. (M.) scutifer*.



Figs 116–122 *Procaviphilus* species, ♂ genitalia. 116, *P. (Meganarionoides) angolensis*. 117, *P. (P.) f. granuloides*. 118, *P. (P.) dubius*. 119, *P. (M.) n. neumanni*. 120, *P. (M.) jordani*. 121, *P. (M.) jordani*, detail of junction of mesomere, paramere and basal apodeme. 122, *P. (M.) serraticus*.

may also contact b.a.l.s. (Figs 116, 117, 119–121); mesomer arch with median extension more or less broad, lateral desclerotisations sometimes apparent (Figs 118, 122)*.

HOSTS. Procaviidae (Hyracoidea) and Cercopithecidae (Primates).

Subgenus *PROCAVIPHILUS* Bedford

(Figs 112, 117, 118)

Procaviphilus Bedford, 1932: 725. Type-species: *Procaviphilus ferrisi* Bedford, by original designation.

DESCRIPTION. Anterior of head of 'procaviphilus' type.

Postcoxae absent or, if present, not greatly developed and not fused to abdominal pleurite II.

Abdominal spiracles all the same size.

Gonapophyses with setal tubercles present but not fused; gonapophyses not apically truncate. Ventral vulval margin expanded, sometimes W-shaped medially, not broadened posteriorly.

Male genitalia with basal apodeme short, attaining abdominal segment VII or VI, lacking median constriction; mesomer arch with lateral desclerotisations.

HOSTS. Procaviidae (Hyracoidea).

SPECIES INCLUDED

dubius Werneck, 1941 (10 ♂, 10 ♀)

ferrisi ferrisi Bedford, 1932 (12 ♂, 5 ♀)

ferrisi granuloides Bedford, 1939 (26 ♂, 19 ♀)

ferrisi hindei Werneck, 1946 (3 ♂, 4 ♀)

granulatus (Ferris, 1930) (13 ♂, 17 ♀)

harrisi Werneck, 1946 (15 ♂, 19 ♀)

robertsi (Bedford, 1928) (16 ♂, 18 ♀)

Subgenus *MEGANARIONOIDES* Eichler

(Figs 110, 111, 113–116, 119–122)

Meganarionoides Eichler, 1940: 159. Type-species: *Trichodectes colobi* Kellogg, by original designation.

Acondylocephalus Werneck, 1941: 478 [as subgenus of *Procavicola* Bedford]. Type-species: *Trichodectes congoensis* Ferris, by original designation. [Synonymy by Werneck, 1946: 85.]

DESCRIPTION. Anterior of head of 'procaviphilus' type or, more frequently, of 'procavicola' type.

Postcoxae of leg III enlarged as described in description of *Procaviphilus* s.l., and fused to abdominal pleurite II, at least in female.

Gonapophyses with setal tubercles absent (in which case gonapophyses characteristically broad and vulval margin produced posteriad as in Fig. 113), or present basally, marginally and submarginally, and fused characteristically to form basal process (Fig. 111); gonapophyses more or less truncate. Ventral vulval margin expanded, as described for *Procaviphilus* s. str. or, more frequently, broadened posteriorly, sometimes produced posteriad (Fig. 113) or with median lobulate process (Fig. 110).

Male genitalia with basal apodeme attaining abdominal segment VII or VI or, more frequently, long, attaining segment III or II, with median constriction (Figs 116, 119); mesomer arch with or without lateral desclerotisation.

HOSTS. Procaviidae (Hyracoidea) and Cercopithecidae (Primates).

COMMENTS. There has been some disagreement in the literature over the correct host of one species in this subgenus. Most species included in *P. (Meganarionoides)* are parasites of Procaviidae, as are all other species in the subfamily Dasyonyginae (other than the three species of *Cebidicola*, which are included in the subfamily for the first time in this study). One species, however, *P. (M.) colobi* (Kellogg, 1910), was described from the monkey *Colobus guereza caudatus* Thomas. Kéler (1938a) included this species with the others described from Primates in his genus *Meganarion* (an objective synonym of *Cebidicola*), although realising that the species were not truly congeneric. Eichler (1940) described the new genus *Meganarionoides* for *colobi*, and placed it with *Cebidicola* and *Lorisicola* in the new subfamily Cebidicolinae. Werneck (1946) recognised the identity of *colobi* with the hyrax lice, and synonymised *Meganarionoides* with *Procavicola (Acondylocephalus)* Werneck, 1941, the subgenus thus taking the name *Procavicola (Meganarionoides)*. Werneck (1946) also suggested that *Colobus* was not the true host of *P. colobi*, but that the louse was probably a parasite of *Dendrohydrax validus* subsp. He suggested that the host record of the type-specimens was erroneous and due to mislabelling (the collection having included

both *Colobus* and *Dendrohyrax*), and that a second record was due to contamination (other hyrax-lice having been associated with the specimens of *colobi*). Hopkins (1949) reported having examined 25 skins of *Colobus polykomos*, which he identified as the 'supposed host', without having found any Trichodectidae, and agreed with Werneck (1946) that *Dendrohyrax validus* subsp. was the correct host. Hopkins & Clay (1952) also identified *D. validus* subsp. as the host, the record from '*Colobus caudatus*' being termed an 'error'. Eichler (1963) agreed, and removed *Meganarionoides* from the Cebidicolinae and placed it in the Dasyonygidae with *Procavicola* (Fig. 38). Emerson & Price (1981) include *P. colobi*, without comment, as a parasite of *Dendrohyrax validus validus*, although the association with the nominate subspecies of this animal has not appeared elsewhere in the literature. Kuhn & Ludwig (1964), however, reported a specimen of *Colobus guereza* with 'hundreds of eggs and adult and larval *Procavicola* on it, all clasping the hairs tightly; most of them on the back and on the throat', and were able to state that the monkey had not been in contact with a *Dendrohyrax* or any other Procaviidae after its death. They concluded 'There is no doubt . . . that *Colobus guereza* is a natural host of *Procavicola* (*Meganarionoides*) *colobi*.' In view of the fact that there are now three records of the species from *Colobus guereza* and none from any member of the Procaviidae, this conclusion seems fully justified.

Meganarionoides was, as described above, treated as a subgenus of *Procavicola* by Werneck (1946). In this he has been followed by most authors, although Eichler (1963) considered it to be a full genus. Before the present study *Meganarionoides* had not been placed as a subgenus of *Procaviphilus*.

SPECIES INCLUDED

- africanus** (Werneck, 1941) **comb. n.** from *Procavicola* (5 ♂, 5 ♀)
angolensis (Bedford, 1936) **comb. n.** from *Procavicola* (8 ♂, 11 ♀)
colobi (Kellogg, 1910) **comb. n.** from *Procavicola* (1 ♂, 1 ♀)
congoensis (Ferris, 1930) **comb. n.** from *Procavicola* (22 ♂, 25 ♀)
jordani (Bedford, 1936) **comb. n.** from *Procavicola* (2 ♂, 2 ♀)
muesebecki (Emerson & Price, 1969) **comb. n.** from *Procavicola* (10 ♂, 10 ♀)
neumanni neumanni (Stobbe, 1913) **comb. n.** from *Procavicola* (2 ♂, 1 ♀)
neumanni baculatus (Ferris, 1930) **comb. n.** from *Procavicola* (13 ♂, 14 ♀)
sclerotis sclerotis Bedford, 1932 [treated as *Procaviphilus* s. str. by previous authors] (10 ♂, 17 ♀)
sclerotis major Maltbaek, 1937 [treated as *Procaviphilus* s. str. by previous authors]
scutifer (Werneck, 1941) **comb. n.** from *Procavicola* (14 ♂, 19 ♀)
serraticus (Hill, 1922) [treated as *Procaviphilus* s. str. by previous authors] (50 ♂, 70 ♀)
tendeiroi (Emerson, 1965) **comb. n.** from *Procavicola* (3 ♂, 2 ♀)

Genus **DASYONYX** Bedford

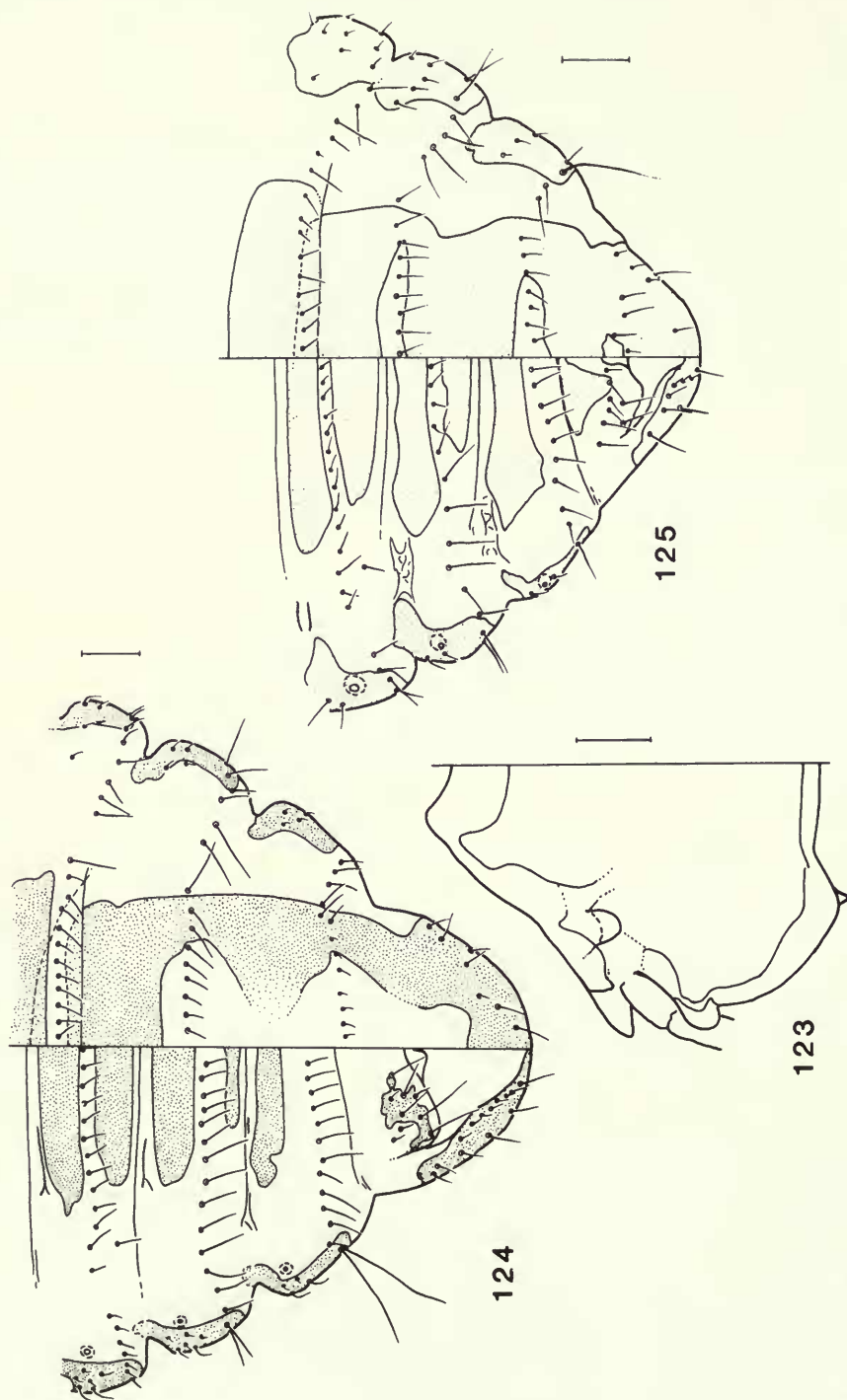
The genus *Dasyonyx* comprises two subgenera.

DESCRIPTION. Anterior of head with osculum present, variable in degree of excavation*; dorsal preantennal sulcus absent; clypeal marginal carina broadened medially, with posterior curvature of broadened portion similar to curvature of osculum* (Fig. 123); conus not large; anterolateral margin of head straight, convex or concave, though not very concave at junction with clypeofrontal suture; preantennal portion of head short or long, outline broadly triangular, trapezoidal or rounded*. Temple margin shallowly convex, sometimes with small rounded projection postero-laterally*. Male scape expanded, with setal row present; male flagellomeres fused, with two basally-articulated 'teeth'; female flagellomeres unfused. Dorsum of head with setae of moderate length. Sitophore sclerite with posterior arms extended (cf. Fig. 12), though sclerite difficult to see.

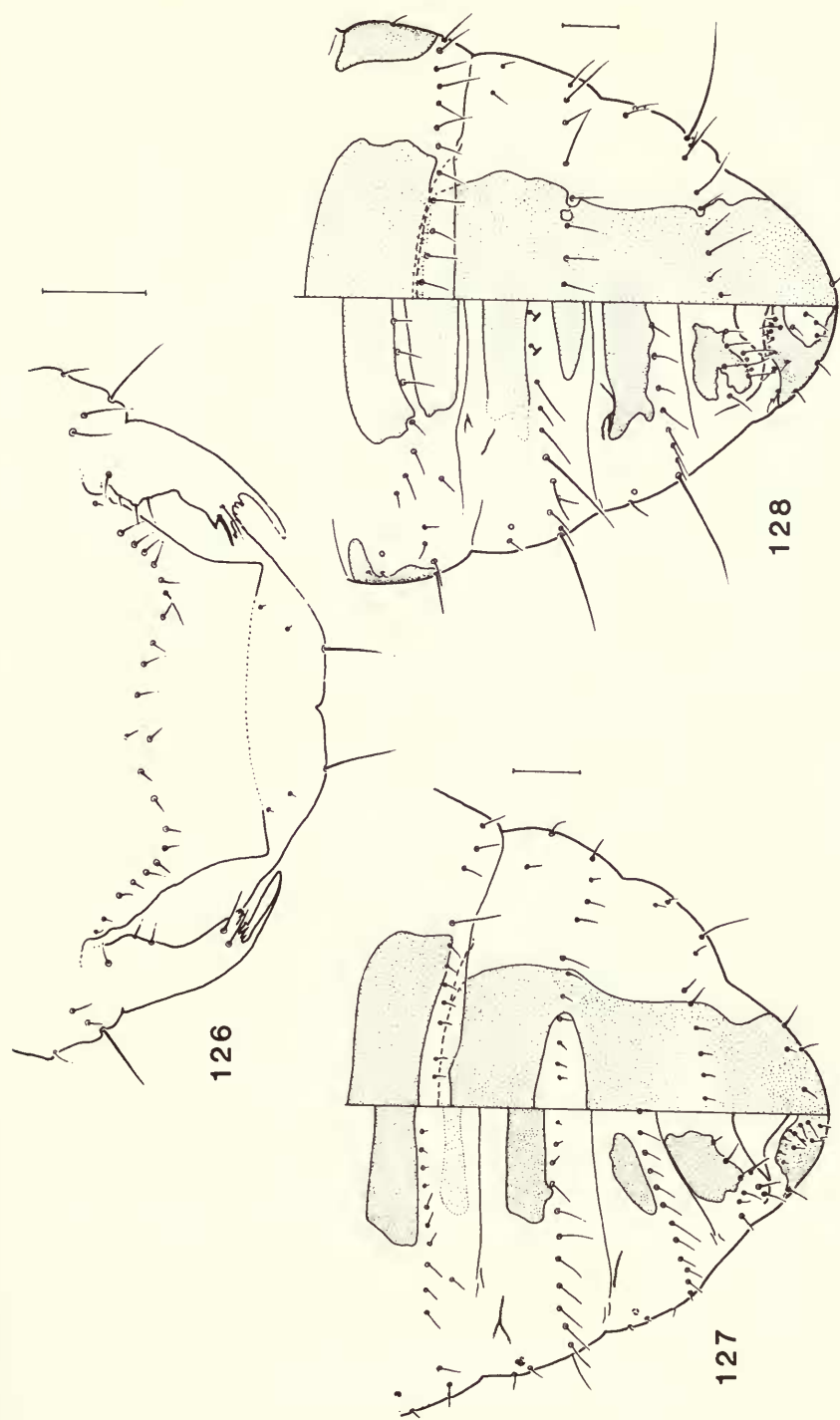
Tarsal claws with ventral spines or teeth (Figs 14, 15)*. Post-coxale of metathoracic leg absent or, if present* enlarged, though not as described for *Procaviphilus* (*Meganarionoides*) and not fused to abdominal pleurite II. Thorax with dorsal setae present only posteriorly on prothoracic margin and posteriorly and posterolaterally on pterothoracic margin; setae short anteriorly, longer posteriorly with the longest setae on the posterolateral margins of the pterothorax; setae generally sparse.

Abdomen broadly oval, with male segment IX not projecting greatly (Fig. 129). Abdominal spiracles present on segments III to VIII, all approximately the same size, frequently inconspicuous. Abdominal setae of moderate length; anterior setae present on pleura only; postero-lateral setae present. Pleural projections present dorsally and ventrally on abdominal pleurum IV, sclerotised. Sclerites present on sterna, terga and pleura (where present) of all abdominal segments except I; male terga, at least of abdominal segment VI, with anterior and posterior sclerites.

Gonapophyses with sparse marginal setae and variably-developed lobe ventrally, the lobe bearing two apical or subapical setae and frequently being serrate along dorsal (posterior) margin (Fig. 126).



Figs 123-125 *Dasyonyx* (*D.*) species. 123, *D. (D.) dendrohyraxis*, ♀ head, dorsal. 124, *D. (D.) dendrohyraxis*, ♂ terminalia. 125, *D. (D.) hopkinsi*, ♂ terminalia.



Figs 126-128 *Dasyonyx* species. 126, *D. (D.) validus ugandensis*, ♀ terminalia, ventral. 127, *D. (D.) ovalis*, ♂ terminalia. 128, *D. (Neodasyonyx) nairobiensis*, ♂ terminalia.

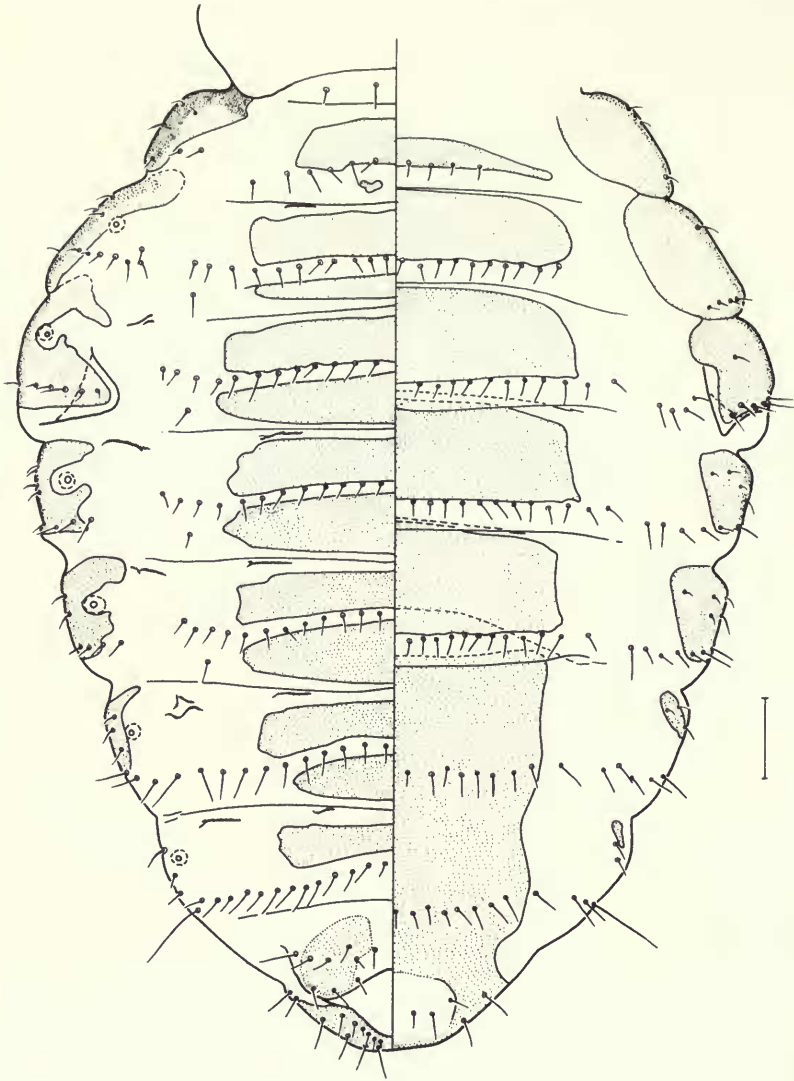


Fig. 129 *Dasyonyx (D.) validus*, ♂ abdomen.

Gonapophyses meet ventral vulval margin acutely, not linked by sclerotised band. Ventral vulval margin not sclerotised; greatly expanded, sometimes with postero-lateral angular projections (Fig. 126); subgenital lobe absent.

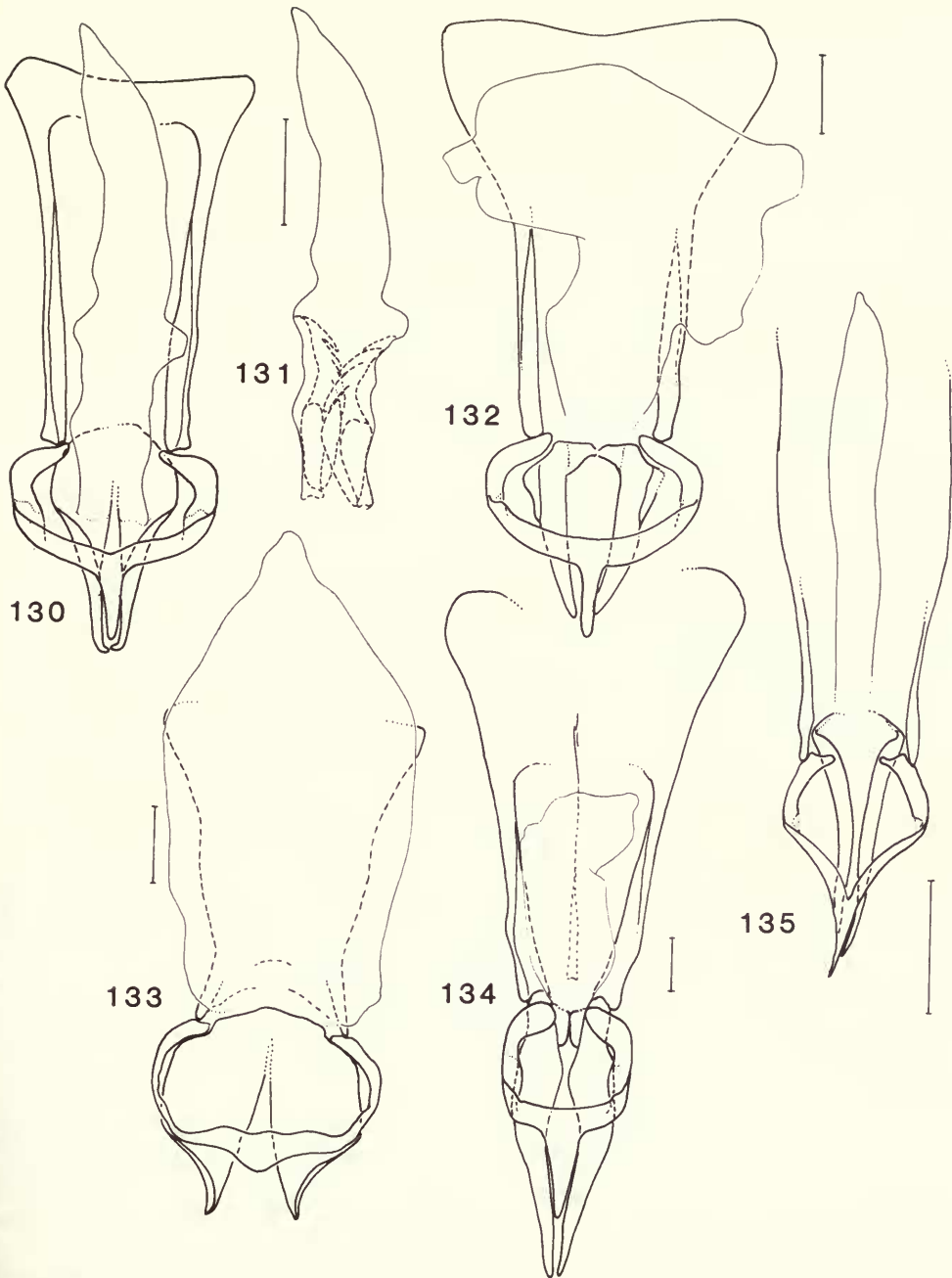
Male subgenital plate with sternites VII, VIII and IX present and fused to s.g.p.r., but variably modified (Figs 124, 125, 127–129), frequently lacking perisetal gap. Pseudostyli absent. Male genital opening postero-dorsal or dorsal. Parameres fused or, if unfused, then with basal flanges (Figs 130, 132, 134, 135). Basiparameral sclerites absent. Mesomeres fused; mesomeral arch with median extension and lateral desclerotisations; mesomeres more or less produced basally between b.a.l.s. to meet parameres, which sometimes do not contact b.a.l.s. (Figs 130, 132–135).

Hosts. Procaviidae (Hyracoidea).

Subgenus *DASYONYX* Bedford

(Figs 14, 123–127, 129–132, 134, 135)

Dasyonyx Bedford, 1932b: 720. Type-species: *Dasyonyx validus* Bedford, by original designation.



Figs 130–135 *Dasyonyx* species, ♂ genitalia. 130, *D. (D.) validus*. 131, *D. (D.) validus*, endophallus, sclerites shown by dashed outlines. 132, *D. (D.) ovalis*, 133, *D. (Neodasyonyx) ruficeps*. 134, *D. (D.) guineensis*. 135, *D. (D.) minor*.

DESCRIPTION. Osculum deeply concave; preantennal outline of male head subtriangular or subtrapezoidal. Temple margin frequently with small rounded projection postero-laterally (Fig. 123).

Tarsal claws with ventral spines slender and sharp (Fig. 14). Postcoxale of metathoracic leg generally present and enlarged, though not as described for *Procaviophilus* (*Meganarionoides*).

Hosts. Procaviidae (Hyracoidea).

SPECIES INCLUDED

- bedfordi* Werneck, 1945 (11 ♂, 16 ♀)
dendrohyracis (Ferris, 1930) (12 ♂, 15 ♀)
guineensis Werneck, 1941 (5 ♂, 3 ♀)
hopkinsi Werneck, 1941 (33 ♂, 32 ♀)
minor Bedford, 1939 (3 ♂, 1 ♀)
oculatus Bedford, 1928
ovalis Bedford, 1932 (36 ♂, 35 ♀)
smallwoodae Emerson & Price, 1969 (7 ♂, 3 ♀)
validus validus Bedford, 1932 (22 ♂, 22 ♀)
validus ugandensis Werneck, 1941 (29 ♂, 26 ♀)

Subgenus *NEODASYONYX* Werneck

(Figs 15, 128, 133)

Neodasyonyx Werneck, 1941: 543 [as subgenus of *Dasyonyx* Bedford]. Type-species: *Dasyonyx transvaalensis* Bedford, by original designation.

DESCRIPTION. Osculum shallowly concave; preantennal region of male head short, outline rounded. Temple margin lacking postero-lateral projection.

Tarsal claws with broad ventral teeth (Fig. 15). Postcoxale of metathoracic leg absent.

HOSTS. Procaviidae (Hyracoidea).

SPECIES INCLUDED

- capensis* Emerson, 1965 (holotype ♂, allotype ♀)
diacanthus (Ehrenberg, 1828) (9 ♂, 8 ♀)
nairobiensis Bedford, 1936 (89 ♂, 92 ♀)
ruficeps Emerson, 1964 (15 ♂, 13 ♀)
transvaalensis Bedford, 1932 (24 ♂, 31 ♀)
waterburgensis Bedford, 1932 (5 ♂, 6 ♀)

Genus *EURYTRICHODECTES* Stobbe

(Figs 9, 16, 136–138)

Eurytrichodectes Stobbe, 1913a: 111. Type-species: *Eurytrichodectes paradoxus* Stobbe, by monotypy.

DESCRIPTION. Anterior of head with osculum absent or, if present, very shallowly concave; dorsal preantennal sulcus absent; clypeal marginal carina slender, not greatly developed medially or, if developed, in the form of a median posteriorly-directed narrow-based triangle; anterolateral margin of head slightly sinuate; preantennal portion of head very short, outline broadly triangular or trapezoid. Temple margin produced posteriorly into broad triangular spike, almost as long as prothorax or, if shorter, attaining front of pronotum (Fig. 138). Male scape expanded, with longitudinal setal row comprising only two setae; male flagellomeres fused, though semicircular sclerite at apex may be vestige of terminal flagellomere; two basally-fused 'teeth' present on male flagellum; female flagellomeres unfused; membranous projection present on female pedicel (Fig. 138). Dorsum of head with setae short, sparse. Sitophore sclerite with posterior arms extended (cf. Fig. 12), though sclerite difficult to see.

Tarsal claws ridged ventrally, lacking teeth or spines (Fig. 16). Postcoxale of metathoracic leg absent. Thorax with dorsal setae present on posterior margin of prothorax and on posterior margin of pterothorax; setae short, sparse.

Abdomen broad and oval, sometimes with male terminal segments tapering and projecting slightly. Abdominal spiracles present on segments III to VIII, all approximately of the same size. Abdominal setae short on sterna IV to IX, terga and pleura, some tergal setae very short; sterna II and III with stout, conical setae (Fig. 136); anterior setae present, sparse on pleura; setal row on terga and sterna may be irregular; postero-lateral setae present. Pleural projections present dorsally and ventrally on abdominal pleurum IV, sclerotised, very long, reaching or almost reaching posterior margin of pleurum V. Sclerites present on sterna, terga and pleura (where present) of all abdominal segments except, sometimes, tergum I; male terga, at least of abdominal segments II to VI, with anterior and posterior sclerites.

Gonapophyses with ventral marginal setae present, each with a small, conical tubercle; ventral lobe absent. Gonapophyses meet ventral vulval margin smoothly, not linked by sclerotised band. Ventral vulval margin not sclerotised; medially expanded and trapezoid; subgenital lobe absent.

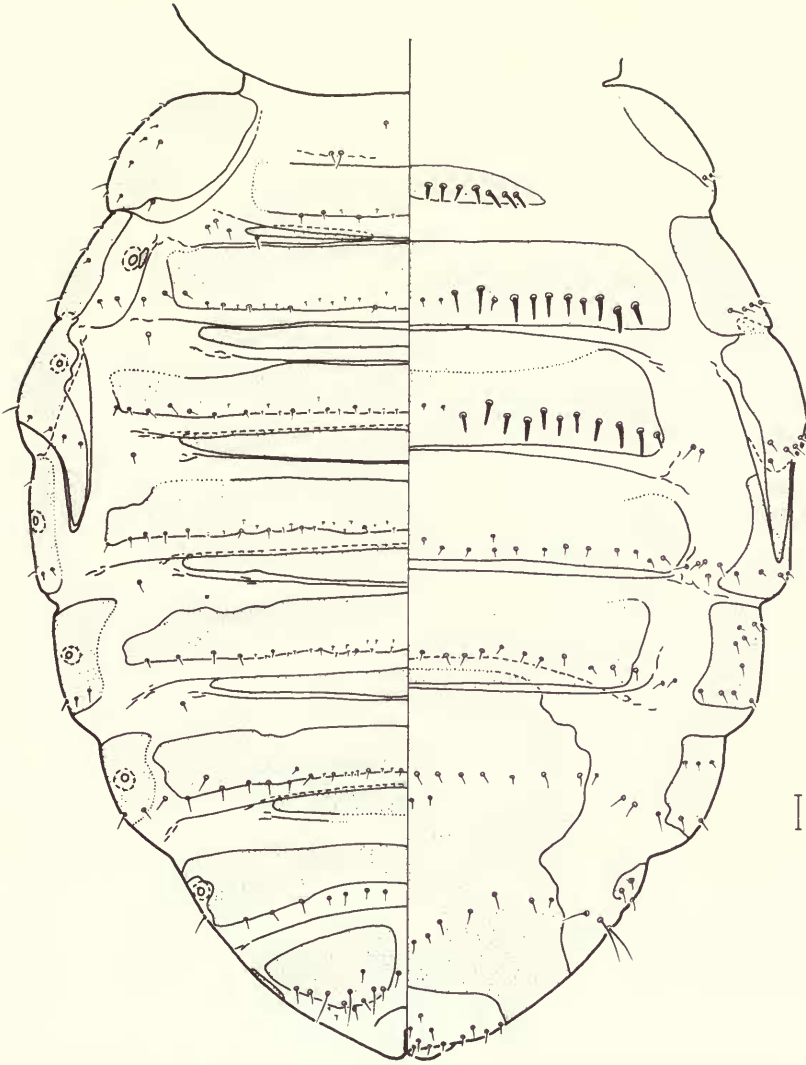


Fig. 136 *Eurytrichodectes paradoxus*, ♂ abdomen.

Male subgenital plate with sternites VII, VIII and IX present and fused to s.g.p.r., with setal gaps very small or absent (Fig. 136). Pseudostyli absent. Male genital opening dorsal. Parameres not fused, sometimes apically bifurcate. Basiparameral sclerites absent. Mesomeres fused; mesomer arch with median extension (see comments below); mesomer arch lacking lateral desclerotisations; mesomeres sometimes produced basally between b.a.l.s. to contact parameres. Male genitalia depicted in Fig. 137.

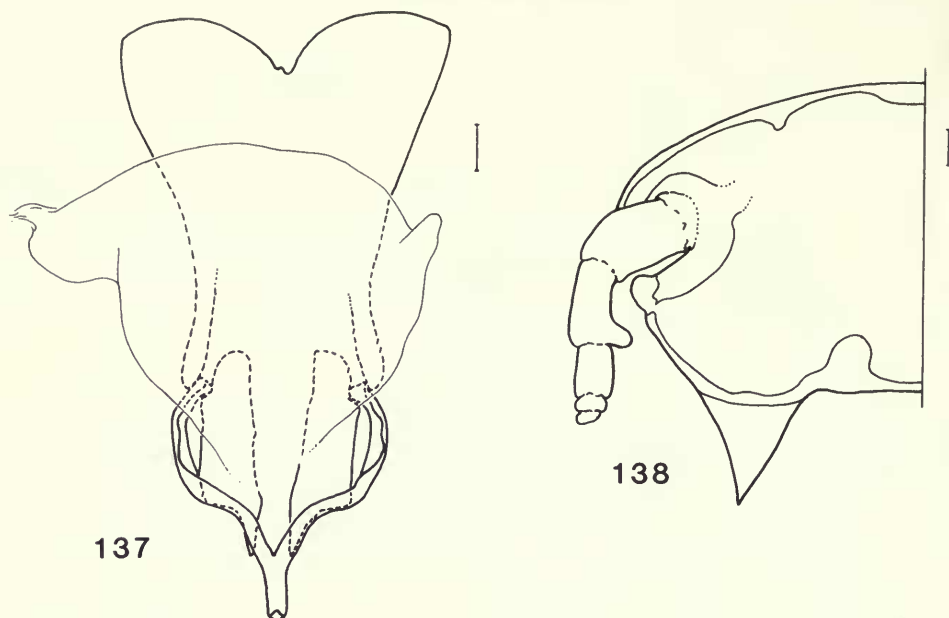
HOSTS. Procaviidae (Hyracoidea).

COMMENTS. The illustration of the the mesomer arch of *E. paradoxus* is reproduced upside-down in Werneck (1941: 452).

SPECIES INCLUDED

machadoi Werneck, 1958 (holotype ♂, allotype ♀)

paradoxus Stobbe, 1913 (29 ♂, 28 ♀)



Figs 137, 138 *Eurytrichodectes paradoxus*. 137, ♂ genitalia. 138, ♀ head, dorsal.

TRICHODECTINAE Kellogg

Genus *PROTELICOLA* Bedford gen. rev.

(Figs 139, 140)

Protelicola Bedford, 1932a: 355. Type-species: *Protelicola intermedius* Bedford, by monotypy.

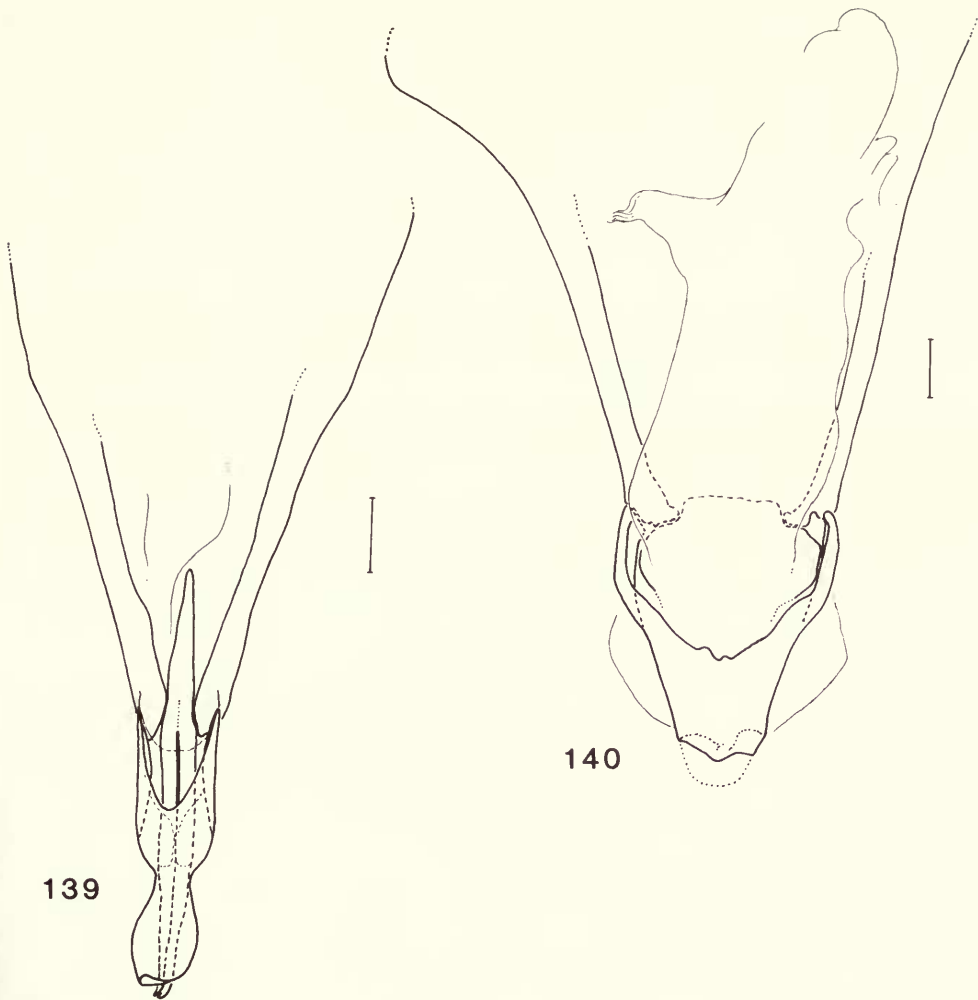
DESCRIPTION. Anterior of head with osculum present; clypeal marginal carina broadened just laterally to osculum, tapering medially and interrupted by dorsal preantennal sulcus; anterolateral margin of head straight or convex; preantennal outline of head triangular or rounded. Temple margin convex. Male scape slightly expanded, with longitudinal setal row present and comprising three or four setae; flagellomeres fused in males and females; male flagellum with two basally-articulated 'teeth'. Dorsal setae of head short or of moderate length, longest and most abundant anteriorly. Sitophore sclerite unmodified.

Thorax with setae long or of moderate length laterally and dorsally, with setae on postero-lateral angles of pterothorax shorter, more spine-like. Prothorax with setae present sparsely on lateral and posterior margins; median gap present, wide; single seta present antero-laterally on disc. Pterothorax with setae present postero-laterally and submarginally posteriorly; median gap present, wide; no setae present on disc.

Abdomen rounded, similar in shape in males and females. Abdominal spiracles present on segments III–VIII. Abdominal setae of moderate length; anterior setae present on pleura only; postero-lateral setae absent. Abdominal pleura lacking projections. Abdominal segments with tergal sclerites absent except tergite IX in female; pleural sclerites present on pleura II and III; sternites IV–VII present in male and V–VII present in female, very slender and difficult to see in both sexes.

Gonapophyses with basal setae and rectangular lobe on ventral margin, lobe formed from more or less fused setal tubercles. Gonapophyses meet ventral vulval margin smoothly, not linked by sclerotised band. Ventral vulval margin not sclerotised. Subgenital lobe present, not marginally serrate, but sometimes with apical papillae. Female genital chamber with small lapped scales on walls, dorsal wall with median longitudinal anterior 'slit' where scales are absent.

Male subgenital plate comprising very slender sternite VII and s.g.p.r. only, s.g.p.r. not reaching posterior of sternum IX. Male genital opening dorsal or postero-dorsal. Pseudostyli absent. Basal apodeme with b.a.l.s. widely divergent anteriorly. Parameres long, slender, fused basally, projecting anteriorly between b.a.l.s. (but see second paragraph of 'comments' below). Basiparameral sclerites



139

140

Figs 139, 140 *Protelicola* species, ♂ genitalia. 139, *P. hyaenae*. 140, undescribed species.

absent. Mesomeres fused apically to form arch, with median projection present, broad (see second and third paragraphs of 'comments' below). Male genitalia depicted in Fig. 139.

Alimentary canal with numerous small spines in crop.

Hosts. Hyaenidae and Protelidae (Carnivora).

COMMENTS. *Protelicola* was treated as a subgenus and a junior synonym of *Felicola* by Hopkins (1949) and Werneck (1948) respectively; its most recent placement (Emerson & Price, 1981) was as a synonym of *Felicola*. A more detailed history of the variations in status of *Protelicola* is presented in Table 5.

In the British Museum (Natural History) collection there is a slide bearing 1 nymphal, 3 female and 2 male (one of which is teneral) lice from *Proteles cristatus termes*. Hopkins has identified the lice as *Protelicola intermedius*. The females are indistinguishable from females of *P. intermedius* s. str., but the male genitalia are very distinct, with the parameres completely fused to form a broad plate, the mesomeral arch wide, and the b.a.l.s. with a small postero-lateral projection contacting the mesomeres (Fig. 140). In all other respects the males resemble *P. intermedius* s. str. It seems that the males represent a new species, differing from *Protelicola intermedius* by the structure of the genitalia, but the identity of the females is doubtful. In view of the limited number of specimens available, the species is not formally described.

Bedford (1932a) described *P. intermedius* from *Proteles cristatus*, the first louse known from a hyaena. Hopkins (1960) described *P. intermedius hyaenae* (in *Felicola*) from *Hyaena brunnea*, distinguishing it from the nominate subspecies by the size, the outline of the preantennal portion of the head, and the male

genitalia. Ledger (1980) raised *P. i. hyaenae* to specific rank although Emerson & Price (1981) retained its subspecific status. Hopkins (1960) indicated three features of the male genitalia in which the two taxa differ: the greater anterior divergence of the b.a.l.s. in *P. i. intermedius*, the shape of the parameres (which he presumed to be completely fused in *P. i. intermedius*, and are only basally fused in *P. i. hyaenae*), and the absence of the mesomeral arch extension in *P. i. intermedius*. The type-series of *P. i. intermedius* has not been seen in the present study, but a series of specimens from *Proteles cristatus* has been examined; these specimens agree with Bedford's and Hopkins' descriptions of *P. i. intermedius* in all but details of the male genitalia. The male genitalia of this series were found to be very similar to those of *P. hyaenae*, with the b.a.l.s. variably divergent anteriorly, the parameres fused only basally and the mesomeral arch with median broad extension (although this is very thinly sclerotised and difficult to see in both taxa). The male genitalia of *P. hyaenae* are depicted in Fig. 139. The two species may be distinguished by the smaller size and shorter preantennal region of *P. hyaenae* (see photographs in Hopkins, 1960).

SPECIES INCLUDED

hyaenae (Hopkins, 1960) **stat. rev.**, **comb. n.** from *Felicola* (holotype ♂, allotype ♀)

intermedius Bedford, 1932 **comb. rev.** from *Felicola* (19 ♂, 48 ♀)

Genus *LUTRIDIA* Kéler

(Figs 141–145)

Lutridia Kéler, 1938a: 433. Type-species: *Trichodectes exilis* Giebel, by original designation.

DESCRIPTION. Anterior of head with osculum absent; dorsal preantennal sulcus absent; clypeal marginal carina broadened medially to form dorsal sclerite with three posteriorly-directed projections (Fig. 142); preantennal portion of head short, outline smoothly rounded. Temple margin convex or rectangular. Male scape not expanded, longitudinal setal row comprising two setae positioned distally on segment; flagellomeres fused in males and females; male flagellum lacking 'teeth'. Dorsum of head with setae short or of moderate length, sparse. Sitophore sclerite unmodified.

Thorax with dorsal setae long or of moderate length, limited to posterior and postero-lateral margins of prothorax and pterothorax.

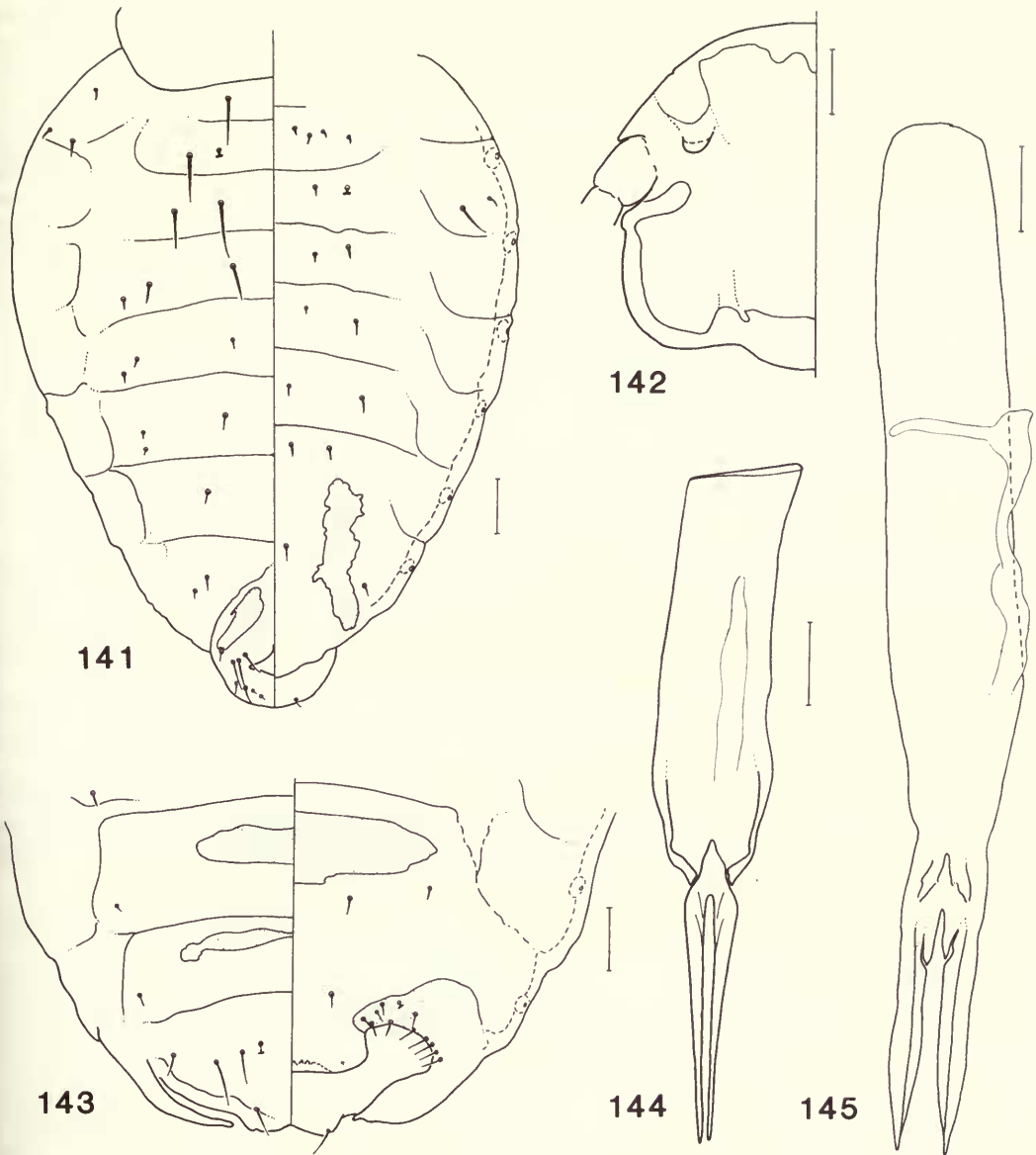
Abdomen oval or slightly elongate-oval, with male segment IX projecting slightly posteriorly (Fig. 141). Abdominal spiracles present on segments III–VIII. Abdominal setae as follows: pleurum II with setae sparse, stout and short, anterior setae and p.s.r. present; pleurum III with setae short and of moderate length, stout, very sparse (*exilis*) or with p.s.r. present (*matschiei*); pleura IV–VII or VIII lacking setae, those on VIII, if present, very small and posteriorly positioned; sternal setae short and stout or longer (about two-thirds length of segment); sternum II with median gap of posterior setal row small or absent; sterna III–IV and VII–VIII (*matschiei*) or III–VIII (*exilis*) with setae very sparse, setae absent from sterna V–VI of *L. matschiei*; terga I–IV (males) or I–III (females) with median setal group including one or two setae as long as segment, other terga with median group absent or comprising shorter setae; terga with lateral seta or setae generally present, of moderate length on terga II–III, shorter on more posterior segments (these setae may represent either lateral setal group or postero-lateral seta); anterior setae present only on pleurum II. Abdominal pleura lacking projections. Sclerites absent from abdominal pleura, present on terga IV–VIII (males) or terga IV–IX (females) and sterna III–VIII (males) or sterna IV–VIII (females); sclerites frequently very faint, may not be seen; male terga lacking posterior sclerites.

Gonapophyses with non-tuberculate setae on ventral margin; ventral lobe not present. Gonapophyses meet ventral vulval margin smoothly, linked by sclerotised band. Ventral vulval margin sclerotised, with chord at 90 degrees to long axis of abdomen, submarginal non-tuberculate setae present. Subgenital lobe present, small, rectangular, sometimes serrate along posterior margin (Fig. 143).

Male subgenital plate comprising s.g.p.r. only or with s.g.p.r. linked by broad sternite VIII (and possibly VII); in either case s.g.p.r. not attaining segment IX. Pseudostyli absent. Male genital opening dorsal. Basal apodeme slender, long, attaining at least abdominal segment III. Parameres long, slender, basally fused; basal fused portion may be partially detached from rest of parameres; parameres sometimes fused to b.a.l.s. Mesomeres absent. Male genitalia depicted in Figs 144, 145.

HOSTS. Lutrinae (Carnivora: Mustelidae).

COMMENTS. *Lutridia* has been treated as a synonym and a subgenus of *Trichodectes* (Hopkins, 1942 and Hopkins, 1949 respectively), though the most recent treatment (Emerson & Price, 1981) considered *Lutridia* as a full genus. The history of the variations in status of *Lutridia* is presented in Table 4.



Figs 141–145 *Lutridia* species. 141, *L. exilis*, ♂ abdomen. 142, *L. matschiei*, ♀ head, dorsal. 143, *L. matschiei*, ♀ terminalia. 144, *L. matschiei*, ♂ genitalia. 145, *L. exilis*, ♂ genitalia.

SPECIES INCLUDED

exilis (Nitzsch, 1861) (3 ♂, 10 ♀)

matschiei (Stobbe, 1913) (36 ♂, 38 ♀)

Genus NEOLUTRIDIA gen. n.

(Figs 146, 147)

Type-species: *Trichodectes lutrae* Werneck.

DESCRIPTION. Anterior of head with osculum absent, though pulvinus attaining margin; dorsal preantennal sulcus absent; clypeal marginal carina slightly broadened medially at junction with pulvinus; preantennal outline broadly and smoothly rounded. Temple margin rectangular. Male scape not expanded; longitudin-

al setal row present, comprising four setae; flagellomeres fused in males and females; male flagellum lacking 'teeth'. Dorsum of head with setae short or of moderate length, sparse; temple margin with two or three longer setae. Sitophore sclerite unmodified.

Prothorax with two setae of medium length on posterior margin; pterothorax with one or two short, spine-like setae anterolaterally and six to ten long setae dorsally on posterior margin.

Abdomen oval, with male segment IX projecting posteriorly. Abdominal spiracles present on segments III–VIII. Abdominal setae as follows: pleurum III with short, stout setae anteriorly and posteriorly; pleura III–VIII lacking setae; terga I–VI (males) or I–IV (females) with central seta of median groups as long as segment, setae otherwise short; terga VII–VIII (males) or V–IX (females) with short setae, sparse; sterna with stout, short setae, sparse; anterior setae present only on pleurum II; postero-lateral setae absent. Abdominal pleura lacking projections. Sclerites absent from abdominal pleura and sterna, but present, slender, on at least terga III–VII (males) or V–IX (females), though may be very faint and not seen; male terga lacking posterior sclerites.

Gonapophyses with small ventral lobes formed from fused setal tubercles. Gonapophyses meet ventral vulval margin smoothly, linked by sclerotised band. Ventral vulval margin sclerotised, with chord at 90 degrees to long axis of abdomen; submarginal non-tuberculate setae present. Subgenital lobe present, large, with lateral spine-like projections and associated setae present basally (Fig. 146).

Male subgenital plate represented by sternite VIII with lateral arms extending anteriad. Pseudostyli absent. Male genital opening dorsal. Basal apodeme attaining abdominal segment III, not slender. Parameres broad, scoop-shaped, not fused together, but fused to b.a.l.s. Mesomeres absent. Male genitalia depicted in Fig. 147.

HOSTS. Lutrinae (Carnivora: Mustelidae).

SPECIES INCLUDED

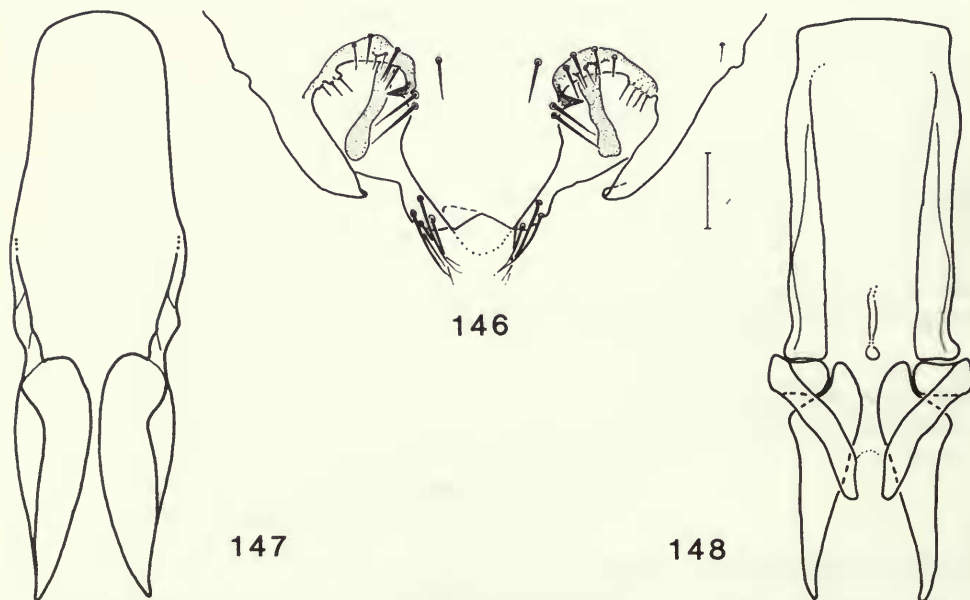
lutrae (Werneck, 1937) **comb. n.** from *Lutridia* (1 ♂, 1 ♀)

Genus *WERNECKODECTES* Conci **gen. rev.**

(Fig. 148)

Werneckodectes Conci, 1946: 59. Type-species: *Trichodectes ferrisi* Werneck, by original designation.

DESCRIPTION. Osculum absent, though pulvinus attains anterior margin of head; dorsal preantennal sulcus present; clypeal marginal carina broadened slightly medially; preantennal portion of head short, outline



Figs 146–148 Trichodectini species. 146, *Neolutridia lutrae*, ♀ terminalia, ventral. 147, *N. lutrae*, ♂ genitalia (after Werneck). 148, *Werneckodectes ferrisi*, ♂ genitalia (after Werneck).

smoothly and broadly rounded. Temple margin convex. Male scape expanded; flagellomeres fused in males and females; male flagellum with two basally-articulated 'teeth' and basal projection. Dorsum of head with setae of moderate length.

Thorax with dorsal setae longest postero-laterally on pterothorax and along posterior margin on pterothorax; shorter setae present submarginally along posterior of pterothorax and on postero-lateral angles of prothorax, where there is a small setal patch; disc and posterior margin of pronotum each with pair of small setae.

Abdomen oval, tapering posteriorly rather more in male than female. Abdominal spiracles present on segments III–VIII. Abdominal setae numerous, anterior setae being present on sterna, terga and possibly pleura of all segments; anterior setae smaller than setae of posterior setal rows on each segment; postero-lateral setae, if present, obscured by large number of other setae. Abdominal pleurum IV with ventral projection in male, possibly with dorsal projection in female; pleurum III possibly with dorsal projection in female. Sclerites present on all abdominal pleura, on terga V–IX (males) or terga VII–IX (females) and on sterna III–VI (males only – sclerites absent on female sterna); male terga without posterior tergites, but anterior tergites, where present, with median longitudinal division.

Gonapophyses with non-tuberculate setae on ventral margin; ventral lobe present, small; setae on lobe stout, short, whilst setae distal to lobe longer, more slender. Gonapophyses meet ventral vulval margin smoothly, linked by broad sclerotised band. Ventral vulval margin sclerotised, with chord at 90 degrees to long axis of abdomen; marginal non-tuberculate setae present, stout, short. Subgenital lobe present, broad, with lateral rounded projections and associated setae present basally.

Male subgenital plate with sternite VII fused to s.g.p.r., sternites VIII and IX absent; s.g.p.r. with sinuate margins. Pseudostyli absent. Male genital opening dorsal. Parameres not as long as basal apodeme, not fused together. Basiparameral sclerites absent. Mesomeres not apically fused, abutting parameres and b.a.l.s. basally. Male genitalia depicted in Fig. 148.

HOSTS. Ursidae (Carnivora).

COMMENTS. *Werneckodectes* has been treated as a synonym and a subgenus of *Trichodectes* (by Hopkins, 1942 and Hopkins, 1949 respectively); its most recent placement was as a synonym of *Trichodectes*. A more comprehensive history of the variations in status of *Werneckodectes* is given in Table 4.

SPECIES INCLUDED

ferrisi (Werneck, 1944) **comb. rev.** from *Trichodectes*.

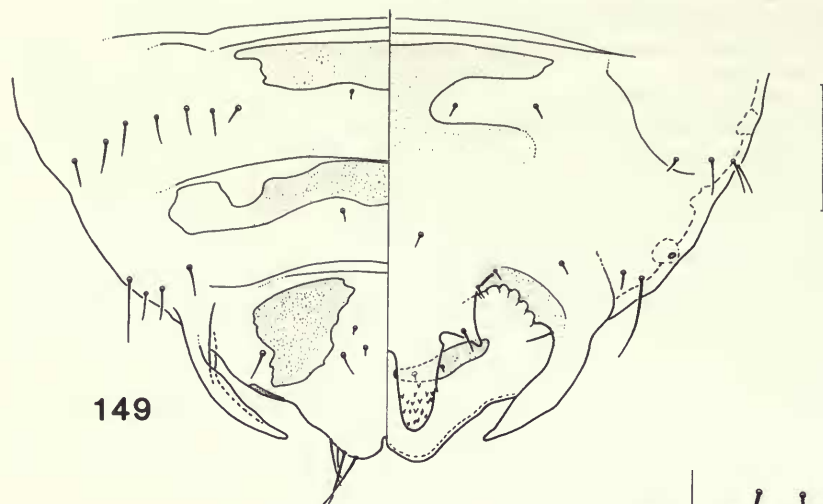
Genus *TRICHODECTES* Nitzsch

The genus *Trichodectes* comprises three subgenera.

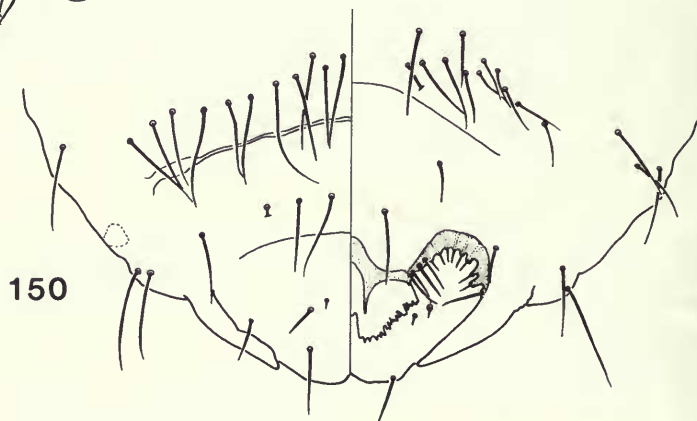
DESCRIPTION. Anterior of head with osculum present or absent*, but always with pulvinus attaining margin; dorsal preantennal sulcus present or absent; clypeal marginal carina broadened to variable extent medially to form simple bar with posterior margin straight or concave, or carina broadened into dorsal sclerite which is heavily-sclerotised laterally (dorsal to margin of clypeus and pulvinus) and lightly or very lightly-sclerotised medially (posterior to the osculum), more or less convex posteriorly or U-shaped with median posterior process*; antero-lateral margin of head straight, convex or sinuate*; preantennal portion of head long or short*, outline broadly rounded, broadly triangular, trapezoid or only slightly produced anteriorly between conia*. Temple margin convex, rectangular or produced laterally*. Male scape expanded or not expanded*; longitudinal setal row present, comprising at least four setae; flagellomeres fused in males and females; male flagellum with one, two or four basally-articulated 'teeth' or 'teeth' absent*. Dorsum of head with setae short, of moderate length or long, longest setae generally present along posterior temple margin; setae sometimes sparse. Sitophore sclerite unmodified.

Thorax with prothoracic dorsal setae sparse, short or of moderate length* posteriorly and postero-laterally, absent from disc; pterothorax with setae on postero-lateral angles short and spine-like or of moderate length, dorsal setae otherwise present on posterior margin only, long or short, numerous, sparse or absent*.

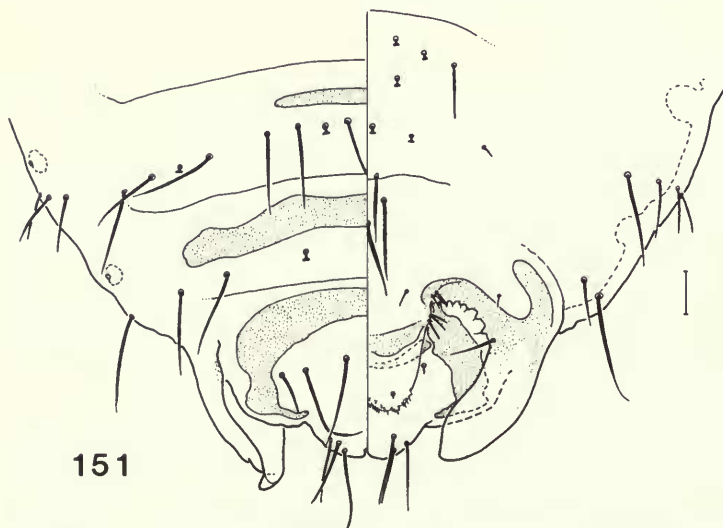
Abdomen oval, male segment IX sometimes slightly projecting posteriorly, but usually positioned dorsally on the abdomen (Figs 156, 158, 160, 164, 165). Abdominal spiracles present on segments III–IV, III–V, III–VII or III–VIII*; spiracle on segment VIII, if present, sometimes much smaller than those on segments III–VII*. Abdomen with at least some tergal and sternal setae as long as segment, or setae very short, sparse and absent from pleura V and VI*; terga with lateral and median groups of setae frequently distinct; tergal setae numerous, or median group reduced to a single seta or absent*; male terga II and III sometimes with median group comprising exceptionally long, stout setae (Fig. 161)*; anterior setae



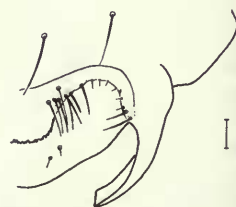
149



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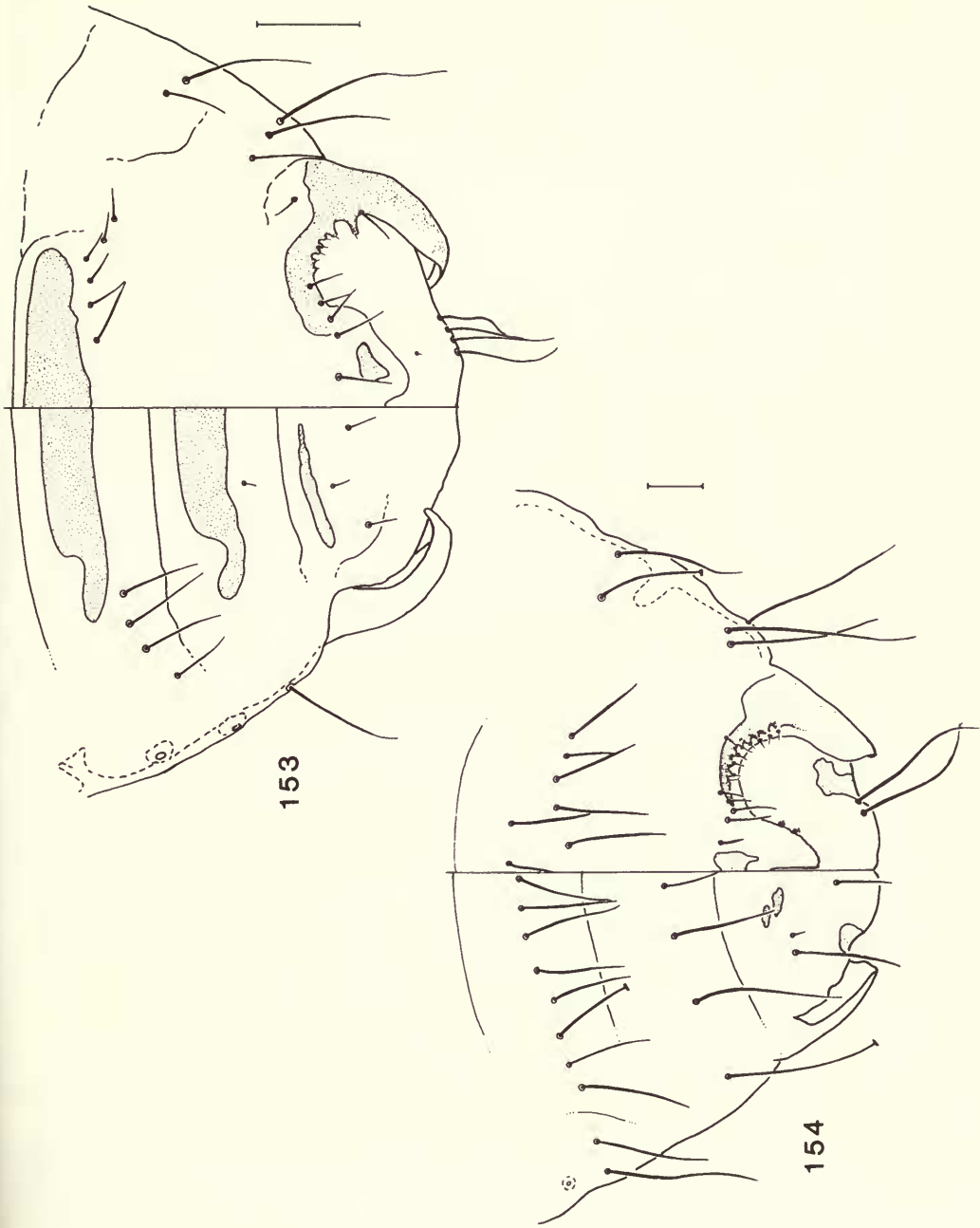


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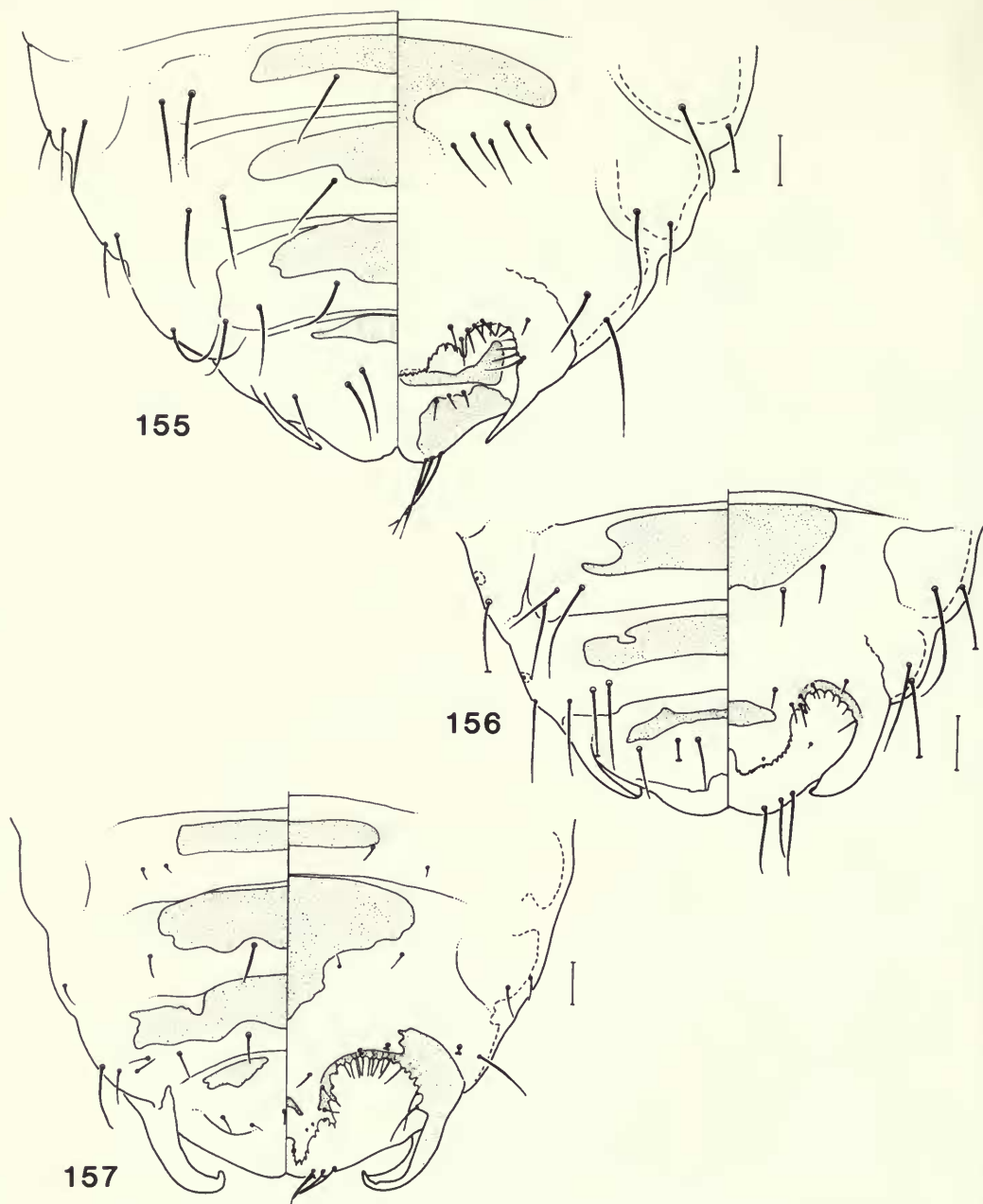


152

Figs 149–152 *Trichodectes* (*T.*) species, ♀ terminalia. 149, *T. (T.) emersoni*. 150, *T. (T.) canis*. 151, *T. (T.) galictidis*. 152, *T. (T.) p. pinguis*, ventral.



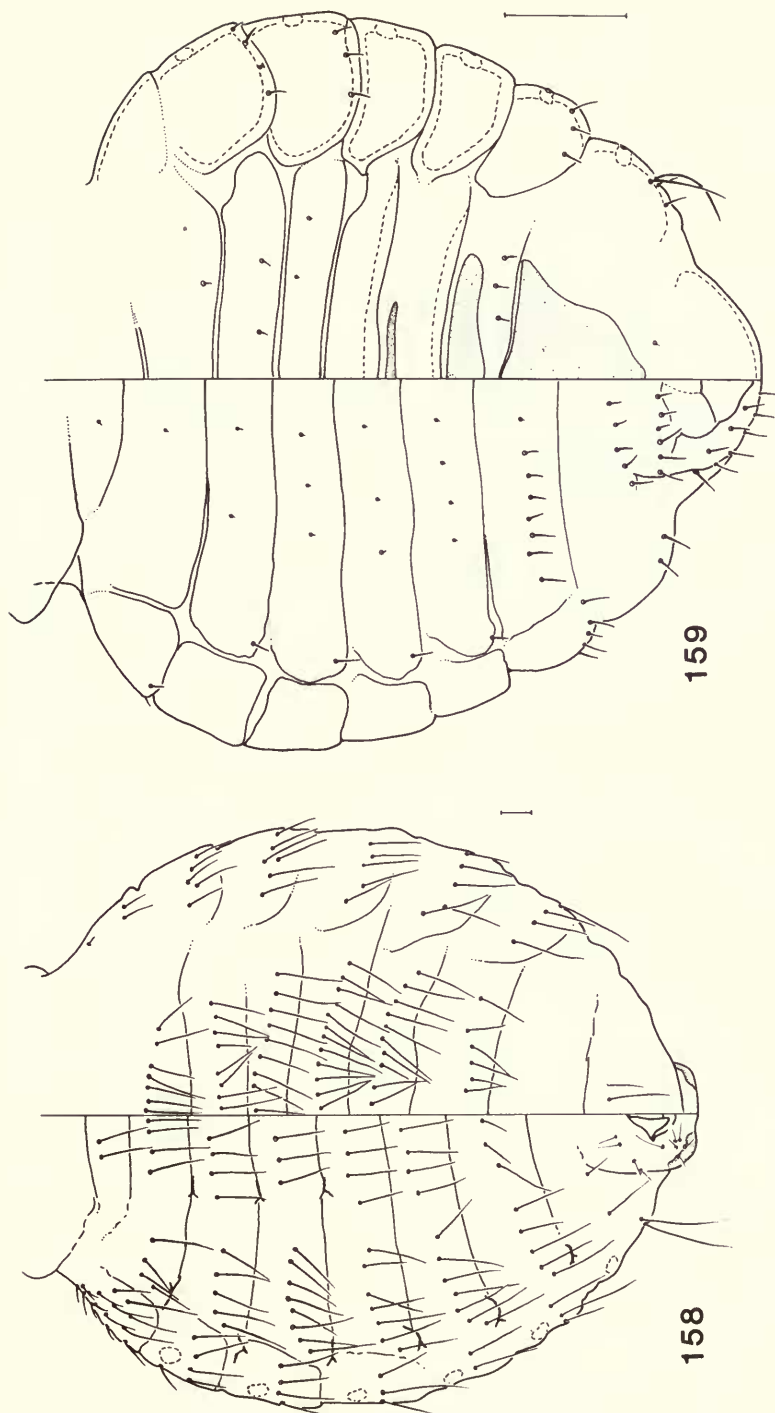
Figs 153, 154 *Trichodectes* species, ♀ terminalia. 153, *T. (Stachiella) emeryi*. 154, *T. (Paratrichodectes) zorillae*.



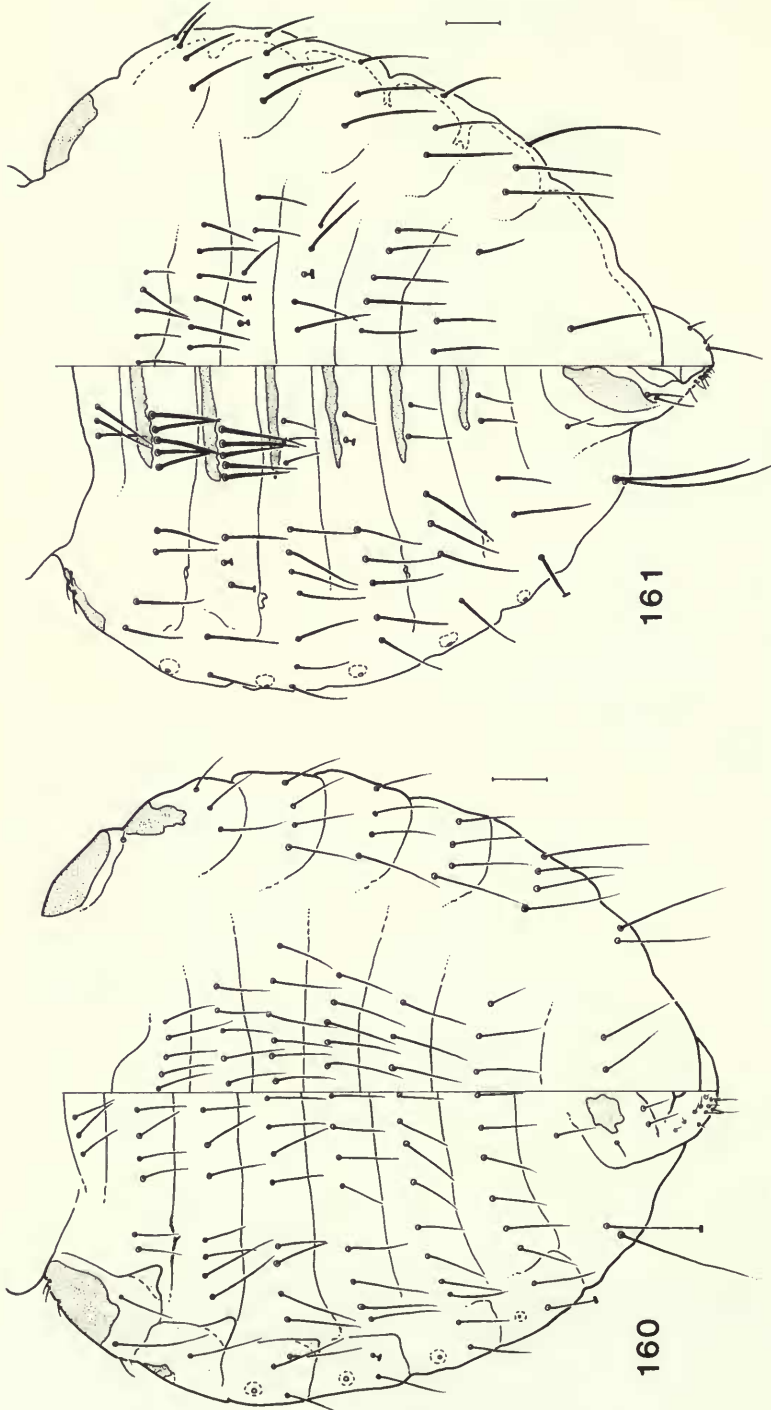
Figs 155–157 *Trichodectes* (*Stachiella*) species, ♀ terminalia. 155, *T. (S.) octomaculatus*. 156, *T. (S.) erminiae*. 157, *T. (S.) potus*.

present only on pleurum II; postero-lateral setae presumed absent, or presence obscured by numerous long setae or reduction (or absence) of lateral setal group. Abdominal pleura lacking projections, or projections present dorsally on pleura II, III and IV* (Fig. 160). Abdominal sclerites variable, present or absent*; male terga with or without anterior and posterior sclerites*.

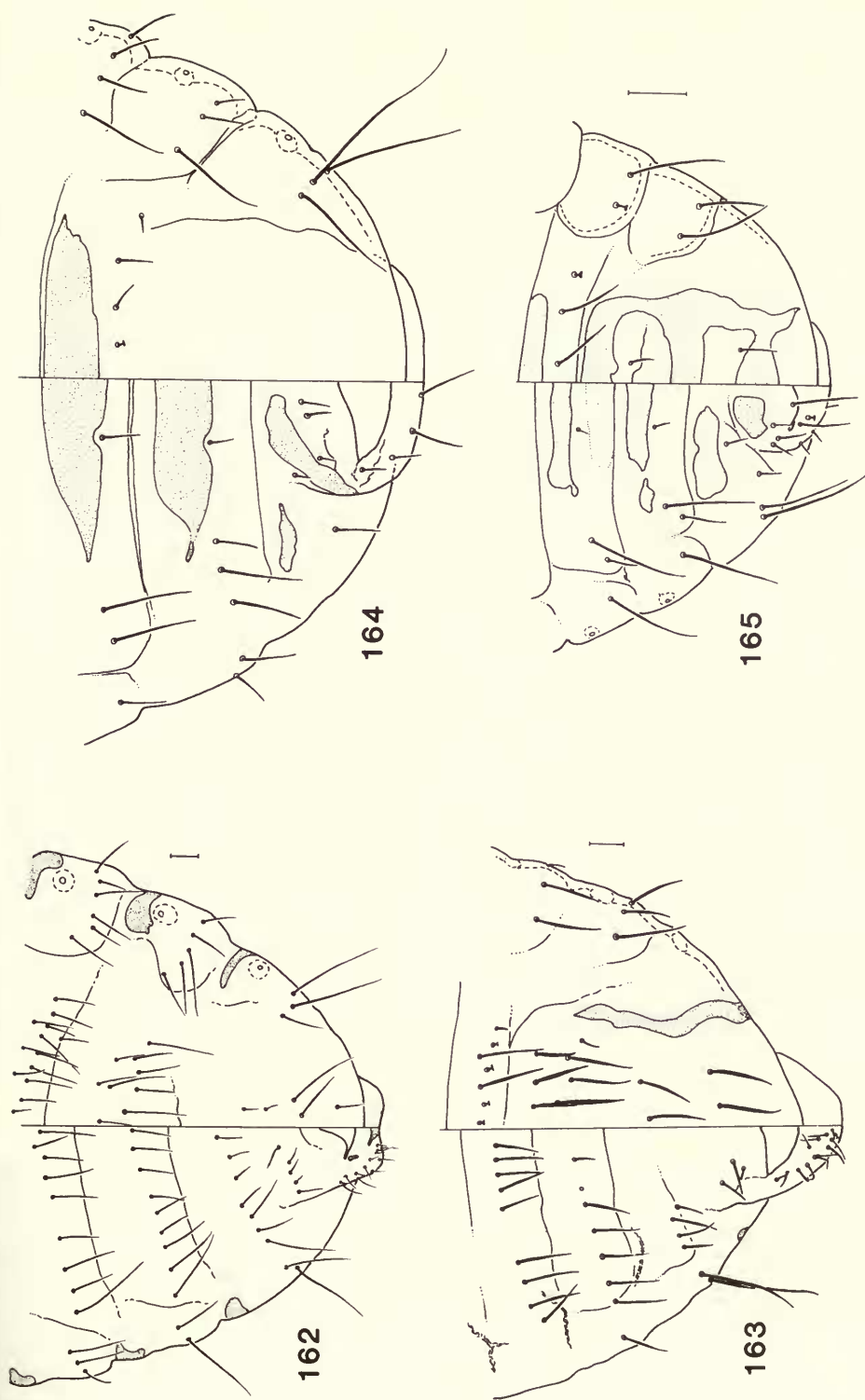
Gonapophyses with separate tuberculate setae and single apical non-tuberculate seta on ventral margin (Figs 149, 151, 153, 156, 159), or tubercles more closely associated (Fig. 155) or all setae non-tuberculate (Figs 152, 154)*; ventral lobe absent. Gonapophyses meet ventral vulval margin smoothly, linked by sclerotised band, or band absent. Ventral vulval margin sclerotised or, rarely, not sclerotised; with chord at



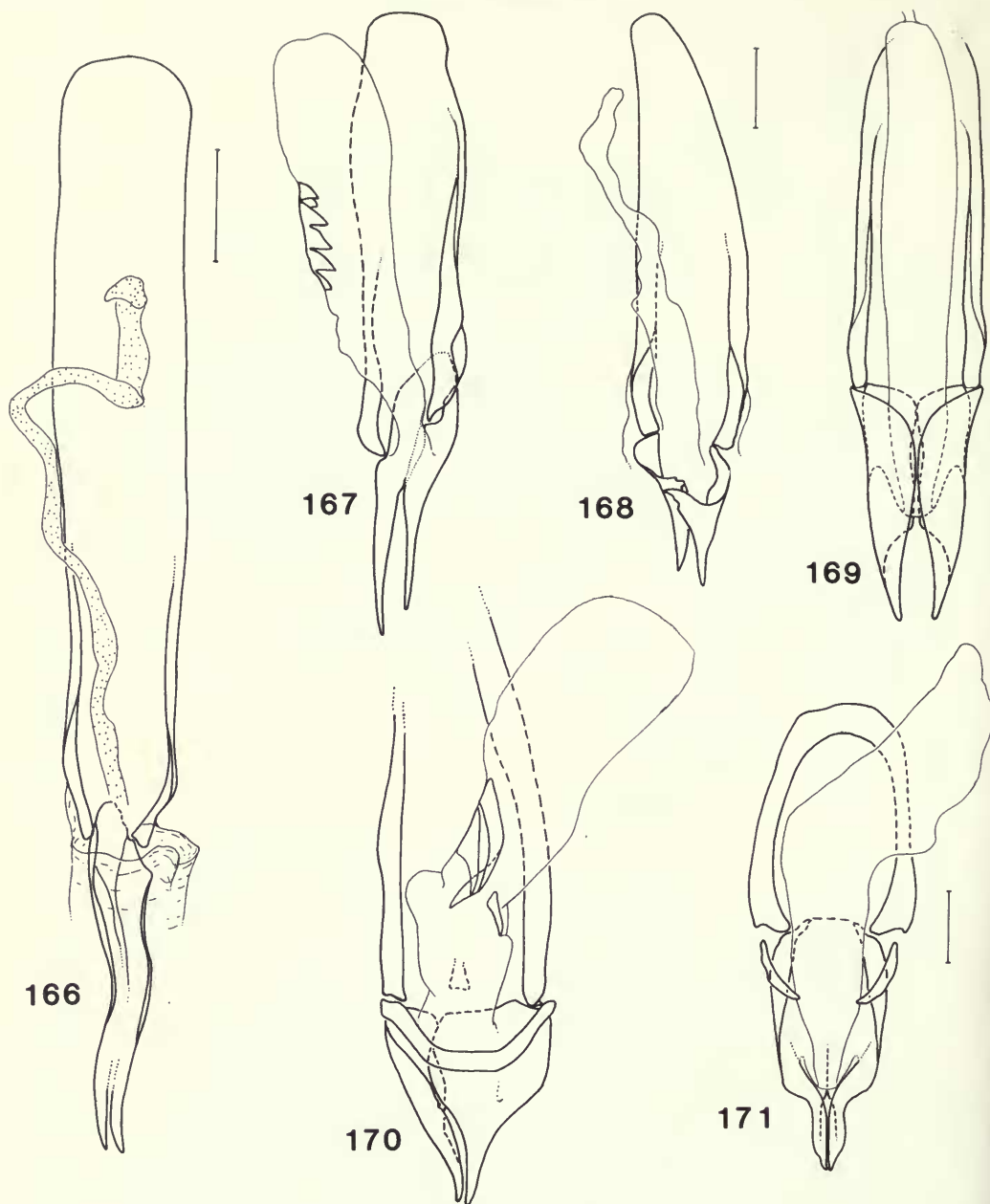
Figs 158, 159 *Trichodectes* (*T.*) species, ♂ abdomens. 158, *T. (T.) canis*. 159, *T. (T.) emersoni*.



Figs 160, 161 *Trichodectes* (*Paratrichodectes*) species, ♂ abdomens. 160, *T. (P.) zorillae*. 161, *T. (P.) ovalis*.



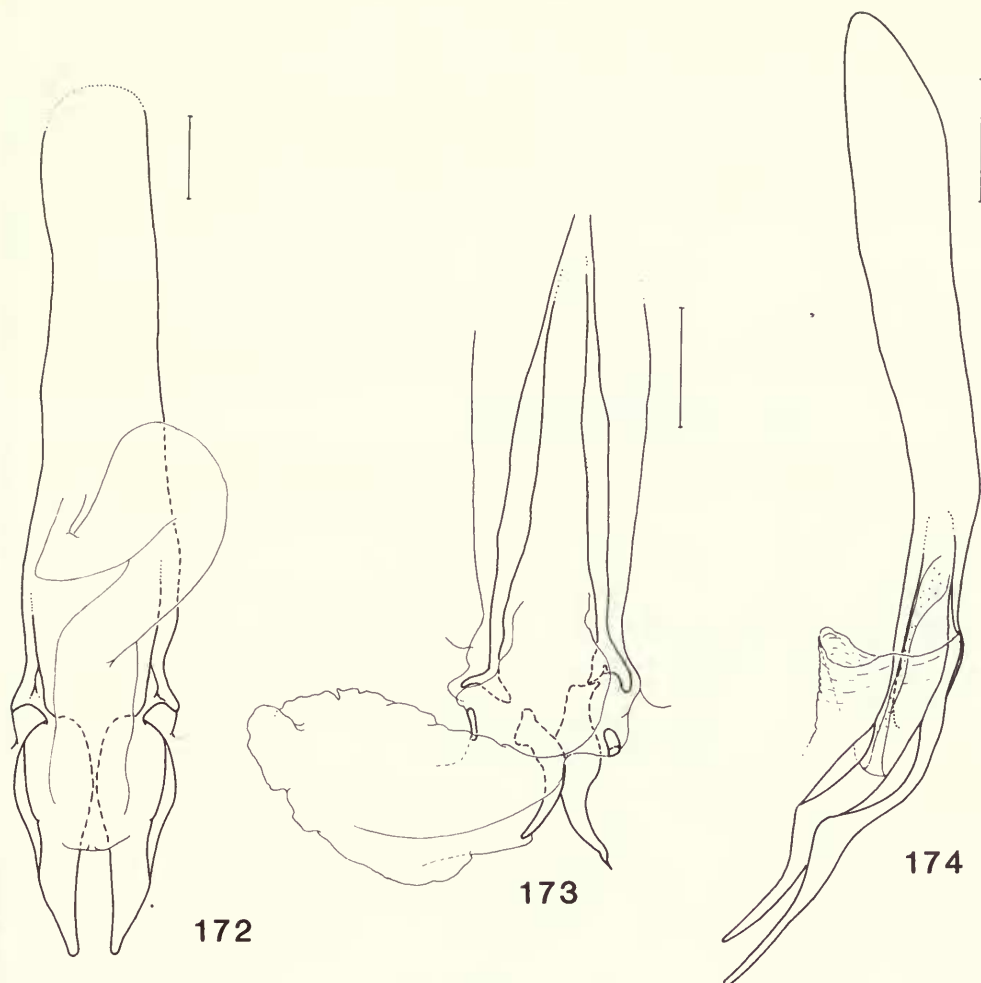
Figs 162-165 *Trichodectes* species, ♂ terminalia. 162, *T. (T.) pinguis euarctidos*. 163, *T. (T.) galictidis*. 164, *T. (Stachiella) emeryi*. 165, *T. (S.) erminiae*.



Figs 166–171 *Trichodectes* species, ♂ genitalia. 166, *T. (Paratrachodectes) ovalis*. 167, *T. (P.) zorillae*. 168, *T. (P.) ugandensis*. 169, *T. (T.) canis*. 170, *T. (T.) galictidis*. 171, *T. (T.) emersoni*.

90 degrees to long axis of abdomen; marginal setae present, tuberculate or non-tuberculate. Subgenital lobe present, usually with marginal serrations and lateral basal projections, the latter sometimes with associated setae.

Male subgenital plate absent (Figs 158, 160–162, 164), represented only by s.g.p.r. (Fig. 163) or enlarged sternite VIII (Fig. 159), with sternites VII, VIII and IX present and fused to s.g.p.r. (Fig. 165), or of the latter form but with sternite VIII divided medially. Pseudostyli absent. Male genital opening dorsal or postero-dorsal. Parameres fused or separate, fused to b.a.l.s. or free*. Basiparameral sclerites absent. Mesomeres absent or present, fused or unfused; if mesomeres fused apically, median extension absent.



Figs 172–174 *Trichodectes* (*Stachiella*) species, ♂ genitalia. 172, *T. (S.) octomaculatus*. 173, *T. (S.) emeryi*. 174, *T. (S.) erminiae*.

HOSTS. Canidae, Mustelidae, Procyonidae, Ursidae and Viverridae (Carnivora).

COMMENTS. The different concepts of the extent of the genus *Trichodectes* held by various workers are summarised in Table 4.

Subgenus *TRICHODECTES* Nitzsch

(Figs 10, 149–152, 158, 159, 162, 163, 169–171)

Trichodectes Nitzsch, 1818: 294. Type-species: '*Trichodectes canis* DeGeer (syn. *T. latus* N.)', by subsequent designation [Johnston & Harrison, 1911: 326].

Ursodectes Kéler, 1938a: 435. Type-species: *Trichodectes pinguis* Burmeister, by original designation. [Synonymy by Hopkins, 1942: 444.]

Grisonia Kéler, 1938a: 464. [No type-species designated] [Homonym of *Grisonia* Gray, 1843: 68].

Galictobius Kéler, 1938b: 228. [Replacement name for *Grisonia* Kéler.] Type-species: *Trichodectes galictidis* Werneck, by original designation. [Synonymy by Hopkins, 1942: 444.]

DESCRIPTION. Male scape expanded; male flagellum with two or four basally-articulated 'teeth'.

Abdominal spiracles present on segments III–VIII, spiracle on segment VIII not smaller than those on anterior segments. Abdomen with at least some tergal and sternal setae as long as segment, or setae very short, sparse and absent from pleura V and VI (*kuntzi* and *emersoni*); male terga II and III sometimes with

median group comprising exceptionally long, stout setae (undescribed sister-species to *T. galictidis*), tergal setae never with median group reduced to single seta or absent (except sometimes on tergum I). Abdominal pleura lacking projections. Abdominal sternal sclerites absent, or present on sterna V–VIII only; abdominal tergal sclerites present or, more usually, absent; if tergites present on male, then not with anterior and posterior sclerites on each segment.

Female genital chamber with ventral wall frequently obscure, dorsal wall bearing sclerotised nodules, sometimes fused together.

Male subgenital plate absent, represented by s.g.p.r. only, or by enlarged sternite VIII only. Parameres fused to form plate or unfused; symmetric or asymmetric; not fused to b.a.l.s. Faintly-sclerotised tongue-like sclerite of uncertain homology sometimes present dorsally between parameres if mesomeres absent (Fig. 169). Mesomeres absent or, if present, fused or unfused. Male genitalia depicted in Figs 169–171.

HOSTS. Canidae, Mustelidae, Ursidae and Viverridae (Carnivora).

COMMENTS. *Trichodectes* Nitzsch, 1818 was placed on the Official List of Generic Names in Zoology, with the type-species *Trichodectes canis* DeGeer, by Opinion 627 of the International Commission of Zoological Nomenclature (1962, *Bulletin of Zoological Nomenclature* 19: 91).

SPECIES INCLUDED

canis (DeGeer, 1778) (c. 100 ♂, c. 100 ♀)

emersoni Hopkins, 1960 (15 ♂, 12 ♀)

galictidis Werneck, 1934 (15 ♂, 16 ♀; also 2 ♂, 1 ♀ of an undescribed sister-species)

kuntzi Emerson, 1964 (15 ♂, 14 ♀)

melis (Fabricius, 1805) (c. 60 ♂, c. 60 ♀)

pinguis pinguis Burmeister, 1838 (1 ♂, 5 ♀)

pinguis euarctidos Hopkins, 1954 (20 ♂, 20 ♀)

vosseleri Stobbe, 1913 (2 ♂, 7 ♀)

Subgenus *PARATRICHODECTES* subgen. n.

(Figs 6, 154, 160, 161, 166–168)

Type-species: *Trichodectes ovalis* Bedford.

DESCRIPTION. Anterior of head with osculum present; clypeal marginal carina broadened medially into dorsal sclerite which is heavily-sclerotised laterally and lightly-sclerotised medially, more or less convex posteriorly or U-shaped with median posterior process; antero-lateral margin of head convex or sinuate; preantennal portion of head not long, outline rounded or subtriangular. Temple margin convex or rectangular. Male scape not greatly expanded; male flagellum with two basally-articulated 'teeth'.

Thorax with prothoracic dorsal setae sparse, of moderate length posteriorly and postero-laterally, absent from disc; pterothorax with setae on postero-lateral angle long dorsally, short and spine-like ventrally; dorsal posterior pterothoracic setae submarginal, long, comprising two pairs with wide median gap.

Abdominal spiracles present on segments III–VII. Abdomen with at least some tergal and sternal setae as long as segment; setae present on all pleura; tergal setae numerous, median group not reduced to a single seta or absent except sometimes on tergum I or on posterior terga of males only, if male terga II and III with median setal group comprising exceptionally long, stout setae; postero-lateral setae presumed absent, though may be present as the most lateral seta of lateral group, which is frequently situated more posteriorly than other setae. Abdominal sterna and terga with or without sclerites; male terga, if sclerites present, with anterior sclerites only.

Female genital chamber with dorsal wall not bearing sclerotised nodules.

Male subgenital plate unsclerotised. Parameres separate or thinly fused to each other; symmetric or asymmetric; not fused to b.a.l.s. Tongue-like sclerite not present. Mesomeres absent. Male genitalia depicted in Figs 166–168.

HOSTS. Mustelinae (Carnivora: Mustelidae).

SPECIES INCLUDED

ovalis Bedford, 1928 **comb. rev.** from *Stachiella* (15 ♂, 12 ♀)

ugandensis Bedford, 1936 **comb. rev.** from *Stachiella* (44 ♂, 47 ♀)

zorillae Stobbe, 1913, **comb. rev.** from *Stachiella* (17 ♂, 26 ♀)

Subgenus *STACHIELLA* Kéler stat. n.

(Figs 153, 155–157, 164, 165, 172–174)

Stachiella Kéler, 1938a: 428. Type-species: *Trichodectes pusillus* Nitzsch [= *Pediculus mustelae* Schrank], by original designation.

Potusdia Conci, 1942: 141. Type-species: *Trichodectes potus* Werneck, by original designation. [Synonymised with *Trichodectes* by Werneck, 1948: 110; **syn. n.** of *Stachiella*.]

DESCRIPTION. Clypeal marginal carina broadened medially into dorsal sclerite which is heavily-sclerotised laterally and lightly or very lightly-sclerotised medially, more or less convex posteriorly or U-shaped with median posterior process; antero-lateral margin of head smoothly convex; preantennal portion of head long or short, outline broadly rounded, sometimes only slightly produced anteriorly between conia. Male scape not, or only slightly, expanded; male flagellum with one or two basally-articulated 'teeth' or 'teeth' absent.

Thorax with prothoracic dorsal setae sparse, of moderate length posteriorly and postero-laterally, absent from disc; pterothorax with setae on postero-lateral angles short and spine-like or of moderate length, dorsal posterior setae submarginal, long, comprising one or more pairs with wide median gap, or absent.

Abdominal spiracles present on segments III–IV, III–V, or III–VIII; spiracle on segment VIII, if present, sometimes much smaller than those on segments III–VII. Abdomen with at least some tergal and sternal setae as long as segment; setae present on all pleura; terga with median setal group of male reduced to a single seta on most segments, lateral group small; female tergal setae of similar arrangement or with median group absent (see discussion on p. 221 above); male terga II and III never with median group comprising exceptionally long, stout setae; postero-lateral setae presumed absent, though perhaps present as the most lateral seta of lateral setal group, which is frequently situated more posteriorly than other setae of the group. Abdominal pleura lacking projections. Abdominal sterna variably sclerotised, with sternites, if present, most commonly on posterior segments; abdominal terga with sclerites present on segments III–VIII or III–IX, sometimes on I and II; male terga frequently with both anterior and posterior sclerites, though posterior sclerites may be faintly-sclerotised or absent; abdominal pleurum II frequently sclerotised, otherwise pleura unsclerotised.

Gonapophyses with separate or closely-associated tuberculate setae and single apical non-tuberculate seta on ventral margin. Gonapophyses meet ventral vulval margin smoothly, linked by sclerotised band. Ventral vulval margin sclerotised. Female genital chamber with dorsal wall not bearing sclerotised nodules.

Male subgenital plate absent, or with sternites VII, VIII and IX present and fused to s.g.p.r., or of this form but with sternite VIII divided medially. Parameres separate or thinly fused to one another; symmetric, asymmetric or asymmetrically deflected; fused or not fused to b.a.l.s. Tongue-like sclerite not present. Mesomeres absent, present, small and unfused, or present and fused. Male genitalia depicted in Figs 172–174.

HOSTS. Mustelidae: Mustelinae and Procyonidae (Carnivora).

COMMENTS. *Stachiella* has been considered a synonym and a subgenus of *Trichodectes* (Hopkins, 1942 and Hopkins, 1949 respectively), although its most recent treatment (Emerson & Price, 1981) was as a valid genus. *Potusdia* has also been considered as a valid genus, subgenus of *Trichodectes* and synonym of *Trichodectes* but has not, before this study, been considered a synonym of *Stachiella*. A more comprehensive history of the variations in status of *Stachiella* and *Potusdia* is given in Table 4.

SPECIES INCLUDED

divaricatus Harrison, 1915 **comb. rev.** from *Stachiella*

emeryi Emerson & Price, 1974 [treated by Emerson & Price (1974, 1981) as *Trichodectes* s. str.] (4 ♂, 17 ♀)

erminiae (Hopkins, 1941) **comb. n.** from *Stachiella* (92 ♂, 100 ♀)

fallax Werneck, 1948 [treated by Werneck (1948) and all subsequent authors as *Trichodectes* s. str.] (2 ♂, 2 ♀)

jacobi (Eichler, 1941) **comb. n.** from *Stachiella*

kingi McGregor, 1917 **comb. rev.** from *Stachiella* (14 ♂, 25 ♀)

larseni (Emerson, 1962) **comb. n.** from *Stachiella* (58 ♂, 57 ♀)

mustelae (Schrank, 1903) **comb. n.** from *Stachiella* (18 ♂, 23 ♀)

octomaculatus Paine, 1912 [treated by all authors as *Trichodectes* s. str.] (48 ♂, 58 ♀)

- potus* Werneck, 1934 [treated by Werneck (1948) and Emerson & Price (1981) as *Trichodectes* s. str.] (19 ♂, 25 ♀)
retusus retusus Burmeister, 1838 **comb. rev.** from *Stachiella* (1 ♂, 1 ♀)
retusus martis (Werneck, 1948) **comb. n.** from *Stachiella* (1 ♂)
retusus salii (Conci, 1940) **comb. n.** from *Stachiella*

Genus *FELICOLA* Ewing

The genus *Felicola* comprises two subgenera.

DESCRIPTION. Anterior of head with osculum present or absent; dorsal preantennal sulcus present or absent; clypeal marginal carina, if osculum absent, with very slight median broadening, or, if osculum present, carina broadened medially into dorsal sclerite which is heavily-sclerotised laterally (dorsal to margin of clypeus and pulvinus) and very lightly-sclerotised medially (posterior to osculum); anterolateral margin of head straight, slightly sinuate or convex; preantennal portion of head long or short, outline triangular or broadly rounded*. Temple margin rectangular or convex. Male scape variably expanded or not expanded*, with longitudinal setal row present and comprising at least three setae; flagellomeres fused in males and females; male flagellum with one or three basally-articulated 'teeth', or variable number of 'teeth' fused to flagellum, or 'teeth' absent*. Dorsum of head with setae short, of moderate length or long, but in any case frequently longer than abdominal tergal setae; setae sparse, though most numerous anteriorly and along lateral margins. Sitophore sclerite unmodified.

Thorax with dorsal setae long or of moderate length though frequently short and spine-like on postero-lateral angles of pterothorax, not present on disc of prothorax or pterothorax.

Abdomen oval or elongate, frequently terminating in more or less acute projection of segment IX in the male (Figs 179, 181, 183–189). Abdominal spiracles absent, or present on segment III, segments III–IV, or segments III–V*. Abdominal setae short, of moderate length, or occasionally long and fine* (Figs 182, 186, 188); male tergum II frequently with 2–6 very long setae medially (Figs 179, 180, 187, 189); abdominal pleurum III frequently with posterior setal row comprising stout, conical setae (Figs 181, 182, 188); anterior setae, if present, only on pleurum II; postero-lateral setae present or absent. Abdominal pleurum III with projections absent, or, if present, dorsal or ventral, sclerotised or unsclerotised; abdominal pleurum IV with projections absent or, if present, dorsal and occasionally ventral, sclerotised or unsclerotised. Abdominal sclerotisation variable; sternal, tergal and pleural sclerites, if present, generally on anterior segments, becoming less clear on posterior segments; male terga sometimes with anterior and posterior sclerites, at least on tergum VI*.

Gonapophyses with non-tuberculate setae and rounded or rectangular lobe present on ventral margin; apical spur present or absent*. Gonapophyses meet ventral vulval margin acutely, not linked by sclerotised band. Ventral vulval margin not sclerotised; straight or concave, with chord less than 90 degrees to long axis of abdomen; subgenital lobe present, apically single or bifurcate, with margins serrate, at least posteriorly (Fig. 175) (see comment below).

Male subgenital plate not present, though sternite VIII sometimes with postero-lateral projections probably homologous with lateral rods of subgenital plate (Fig. 181). Pseudostyli absent. Male genital opening postero-dorsal or dorsal; segment IX frequently produced posteriad. Parameres generally long and slender (Figs 191, 192, 197, 201), occasionally broader (Fig. 198); frequently fused completely or, more usually, basally only. Basiparameral sclerites absent. Mesomeres present or absent; if present, unfused (Fig. 200) or, if fused, median extension absent*. Male genitalia depicted in Figs 190–206.

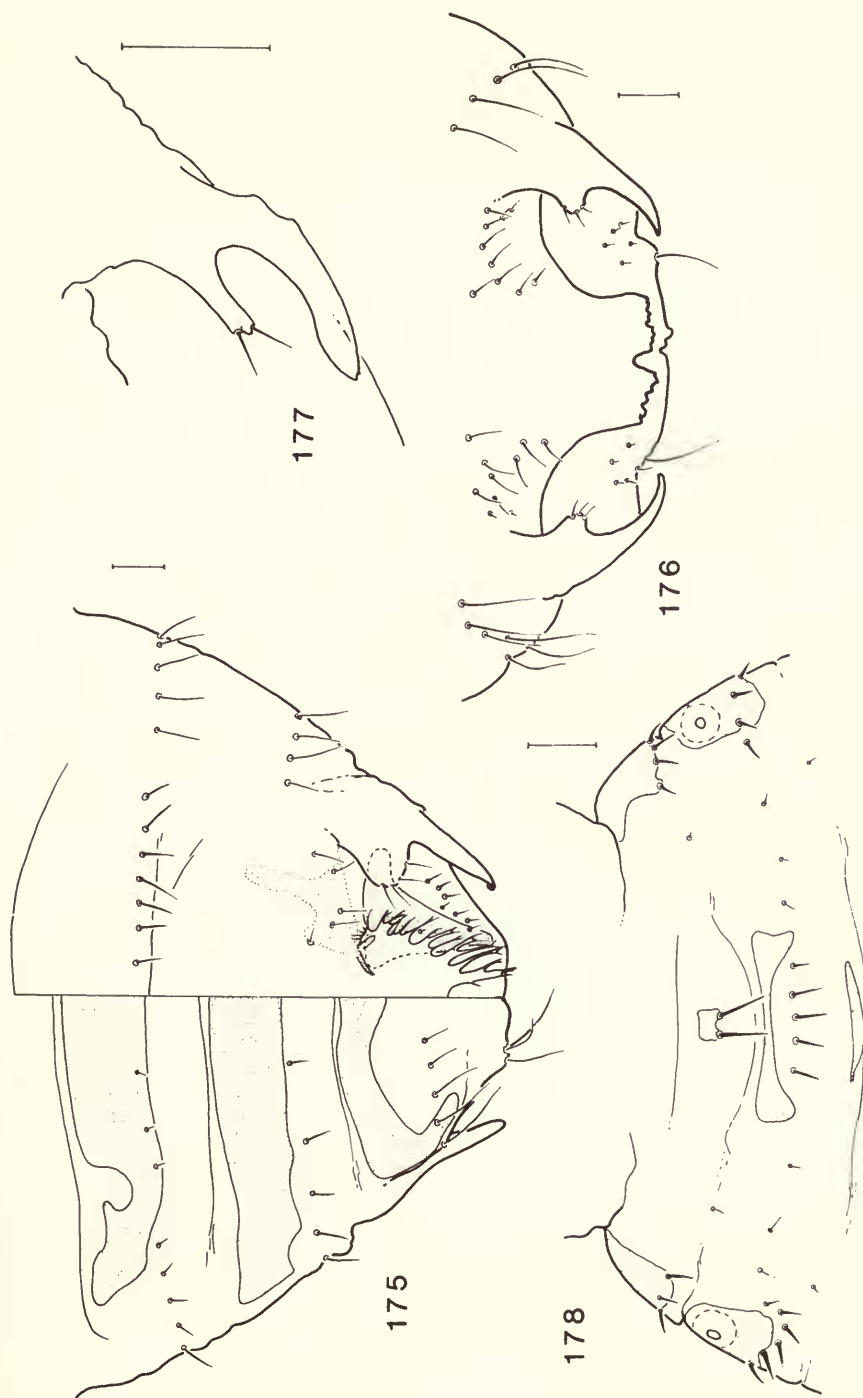
HOSTS. Herpestidae, Viverridae, Felidae and Canidae (Carnivora).

COMMENTS. Emerson & Price (1980) distinguish the females of their new species *Suricatoecus occidentalis* (transferred to *Felicola* in this study) from other species in the '*helogale* Group' (equivalent to the *congoensis-occidentalis* clade) by the presumed absence of the subgenital lobe in *occidentalis*. Examination of the type-series of this species, however, reveals that the subgenital lobe, although very fine, is present in all the females. A second species of this clade, close to *F. helogaloidis*, has been taken from skins of *Crossarchus obscurus* (the host of *F. occidentalis*) and specimens are in the collection of the British Museum (Natural History).

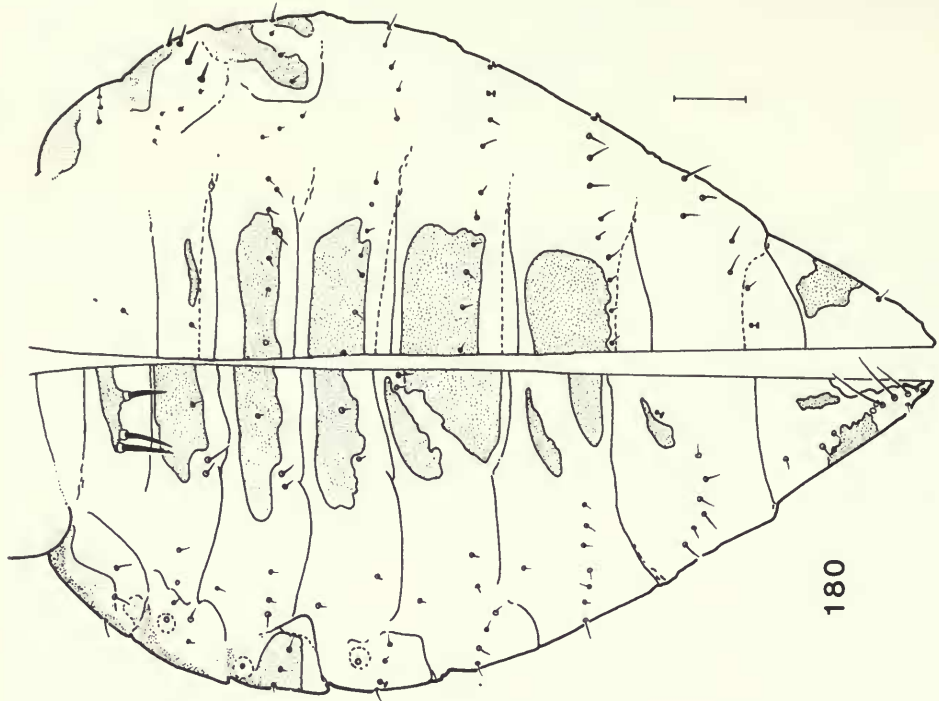
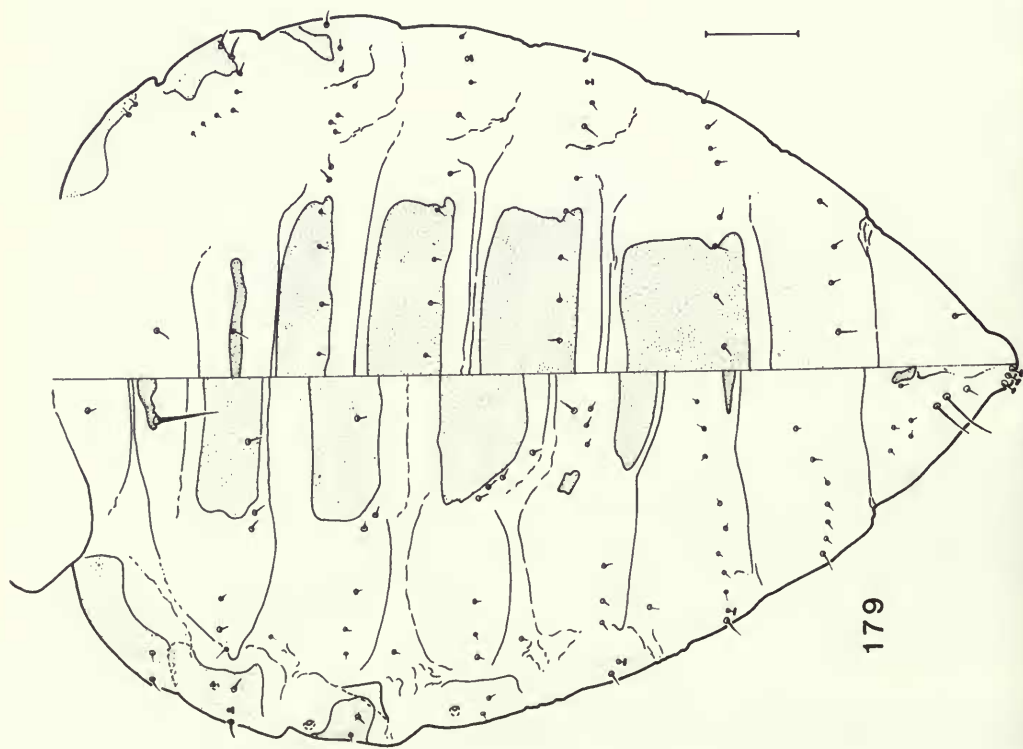
Subgenus *FELICOLA* Ewing

(Figs 5, 175, 179–185, 190–193, 196–198, 202–204)

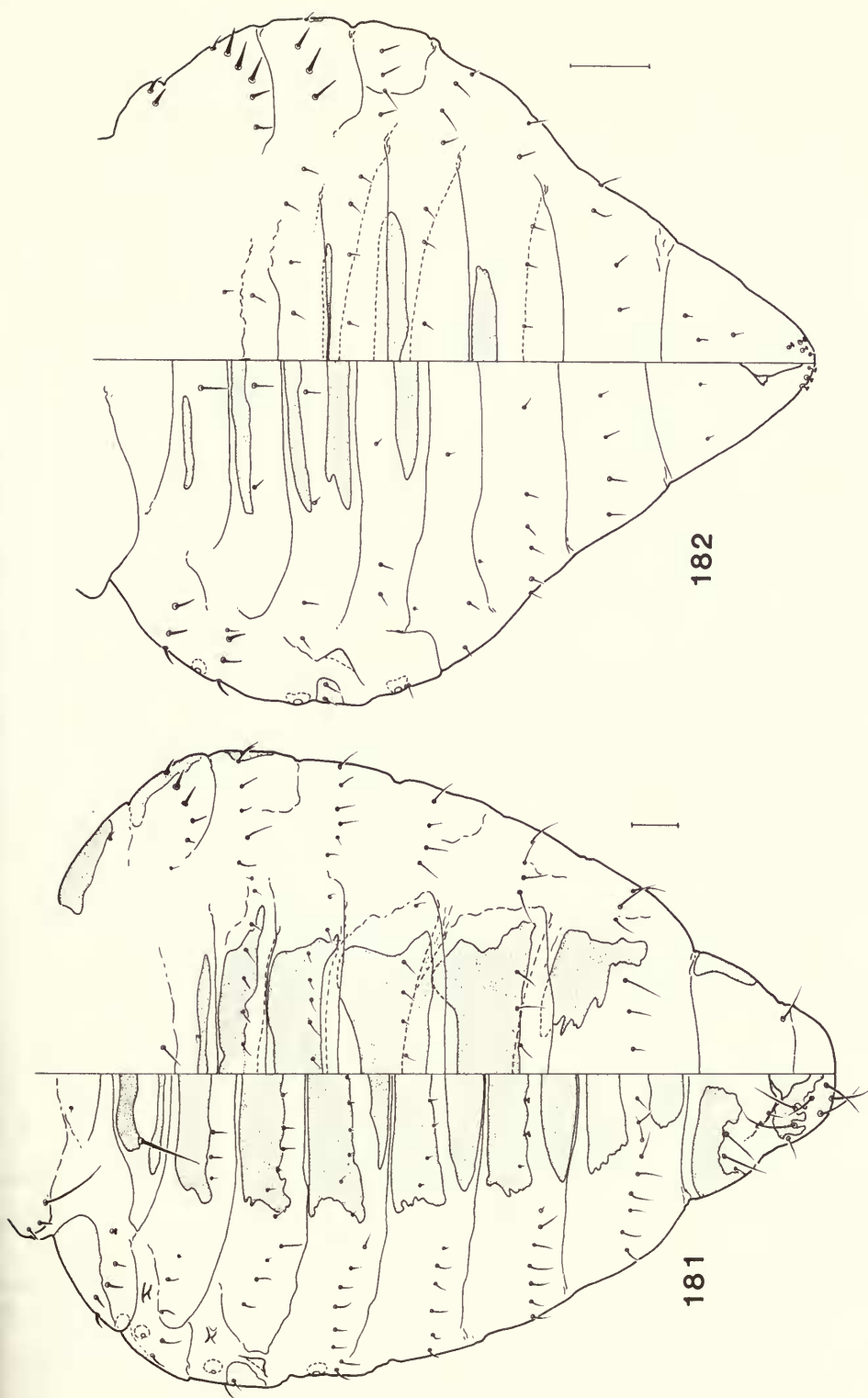
Felicola Ewing, 1. vi. 1929: 121, 122, 192. Type-species: *Trichodectes subrostratus* Burmeister [attributed to Nitzsch], by original designation.



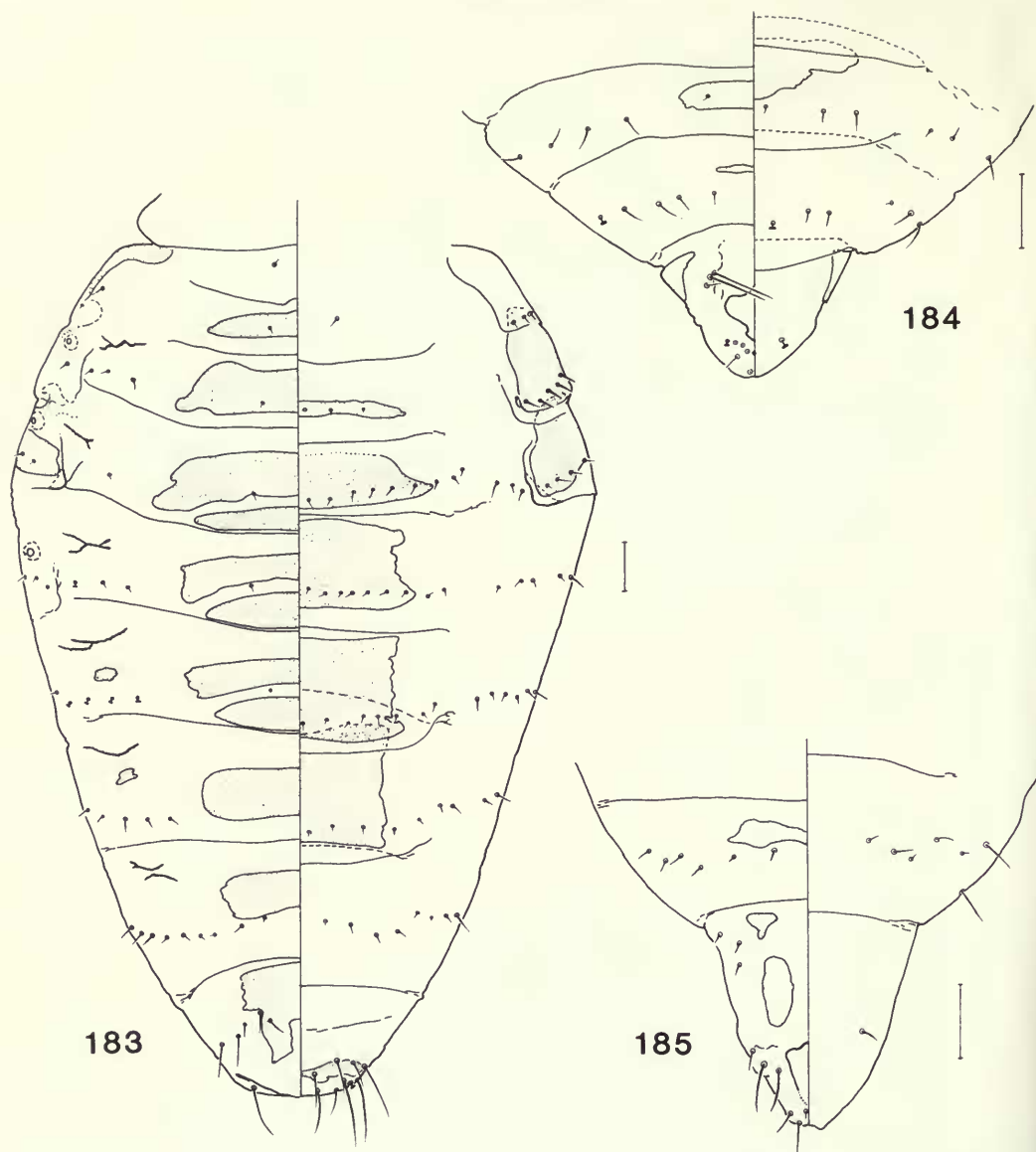
Figs 175-178 *Felicola* species. 175, *F. (F.) zeylonicus*, ♀ terminalia. 176, *F. (Suricatoecus) vulpis*, ♀ terminalia, ventral. 177, *F. (S.) decipiens*, ♀ gonapophysis, ventral. 178, *F. (S.) pygidialis*, ♂ abdominal terga I-III.



Figs 179, 180 *Felicola (F.)* species, ♂ abdomens. 179, *F. (F.) cynicitis*. 180, *F. (F.) setosus*.



Figs 181, 182 *Felicola (F.)* species, ♂ abdomens. 181, *F. (F.) congoensis*. 182, *F. (F.) minimus*.



Figs 183–185 *Felicola* (F.) species. 183, *F. (F.) calogaleus*, ♂ abdomen. 184, *F. (F.) helogale*, ♂ terminalia. 185, *F. (F.) hopkinsi*, ♂ terminalia.

Felicinia Bedford, -x.1929: 519. Type-species: *Trichodectes subrostratus* Burmeister [attributed to Nitzsch], by original designation. [Synonymised by Bedford, 1932a: 536.]

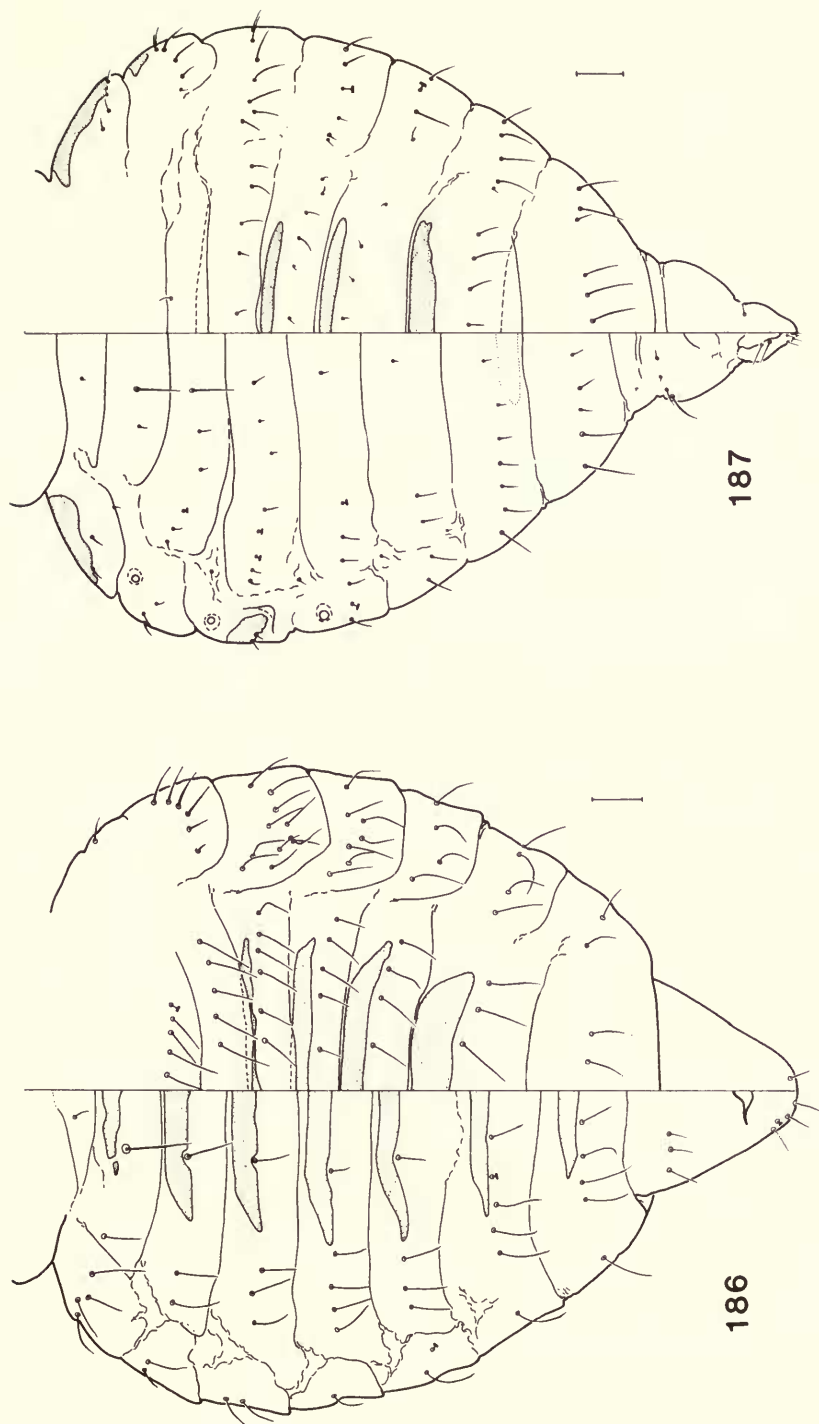
Bedfordia Kéler, 1938a: 463. Type-species: *Felicola helogale* Bedford, by original designation. [Homonym of *Bedfordia* Fahrenholz, 1936: 55.] [Synonymised with *Felicola* by Hopkins, 1941: 36.]

Fastigatosculum Kéler, 1939: 11. [Replacement name for *Bedfordia* Kéler.] [Synonymised with *Suricatoecus* by Werneck, 1948.]

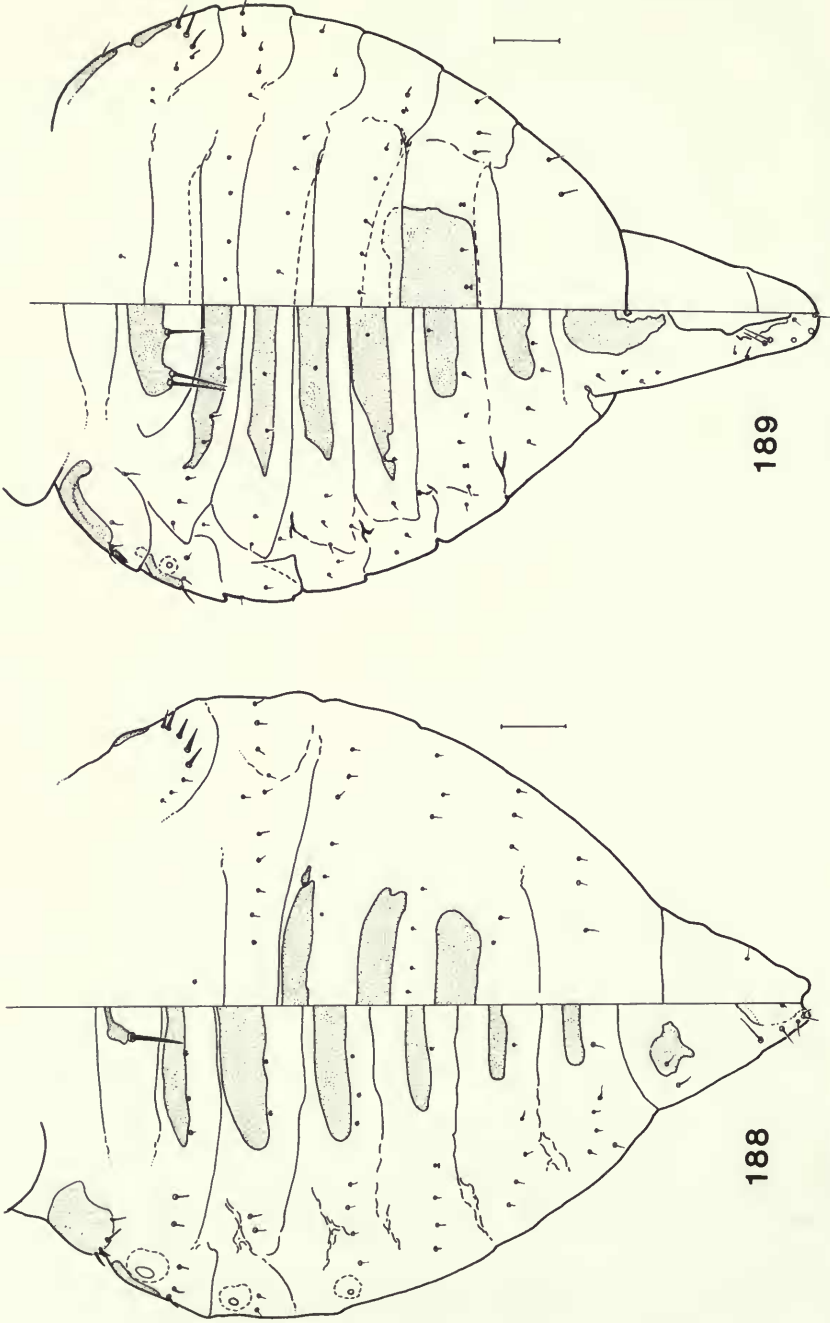
DESCRIPTION. Preantennal portion of head with outline narrowly or broadly triangular or rounded. Male flagellum with 'teeth' absent or, if present, numbering one, two, three or four and fused to flagellum, not basally articulated.

Abdominal spiracles absent, or present on segments III–IV or III–V. Abdominal setae very short or of moderate length.

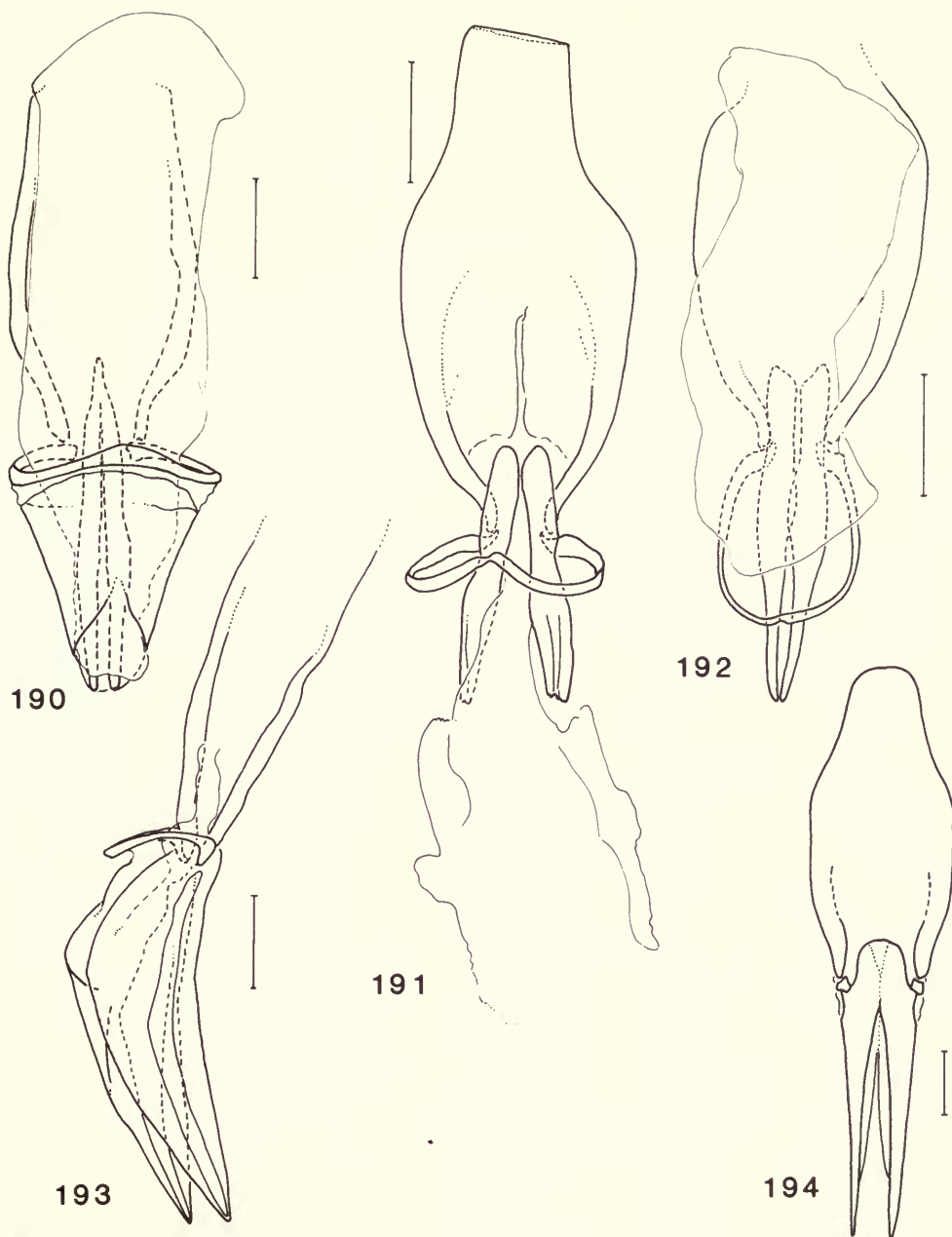
Gonapophyses with rounded lobe on ventral margin; spur present or absent.



Figs 186, 187 *Felicola (Suricatoecus) fahrenheitzi*. 186, F. (S.) *fahrenheitzi*. 187, F. (S.) *decipiens*.



Figs 188, 189 *Felicola* (*Suricatoecus*), ♂ abdomens. 188, *F. (S.) acuirostris*. 189, *F. (S.) bedfordi*.

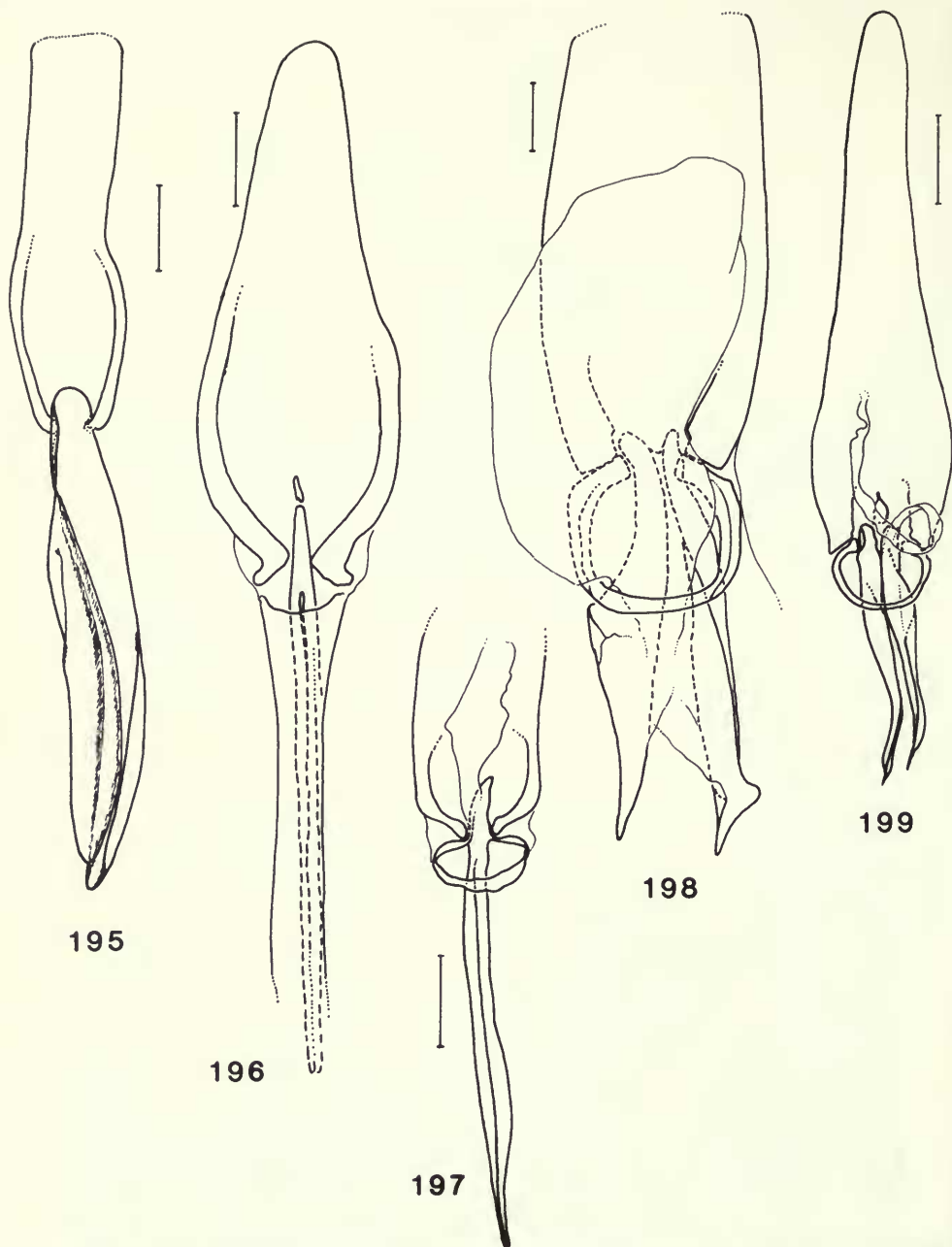


Figs 190–194 *Felicola* species, ♂ genitalia. 190, *F. (F.) calogaleus*. 191, *F. (F.) inaequalis*, endophallus partially everted. 192, *F. (F.) inaequalis*, endophallus not everted. 193, *F. (F.) setosus*; 194, *F. (Suricatoecus) fahrenheitsi*.

Everted portion of endophallus frequently thinly sclerotised (Figs 190, 196, 204). Mesomeres present and fused or absent.

Hosts. Felidae, Herpestidae and Viverridae (Carnivora).

COMMENTS. *F. genettae* (Fresca) is included on the basis of the figures and description of Fresca (1924) which, although poor, suggest an affinity with the *calogaleus-viverriculae* clade. If this is a correct placement, the host record of *Genetta genetta rhodanica* is anomalous. The various treatments of the junior



Figs 195–199 *Felicola* species, ♂ genitalia. 195, *F. (Suricatoecus) bedfordi*. 196, *F. (F.) robertsi*. 197, *F. (F.) hopkinsi*. 198, *F. (F.) congoensis*. 199, *F. (F.) helogale*.

synonyms of *Felicola* are summarised in Table 5; omitted from the table is Conci (1946) who, like Eichler (1941, 1963) regarded *Fastigatosculum* as a valid genus.

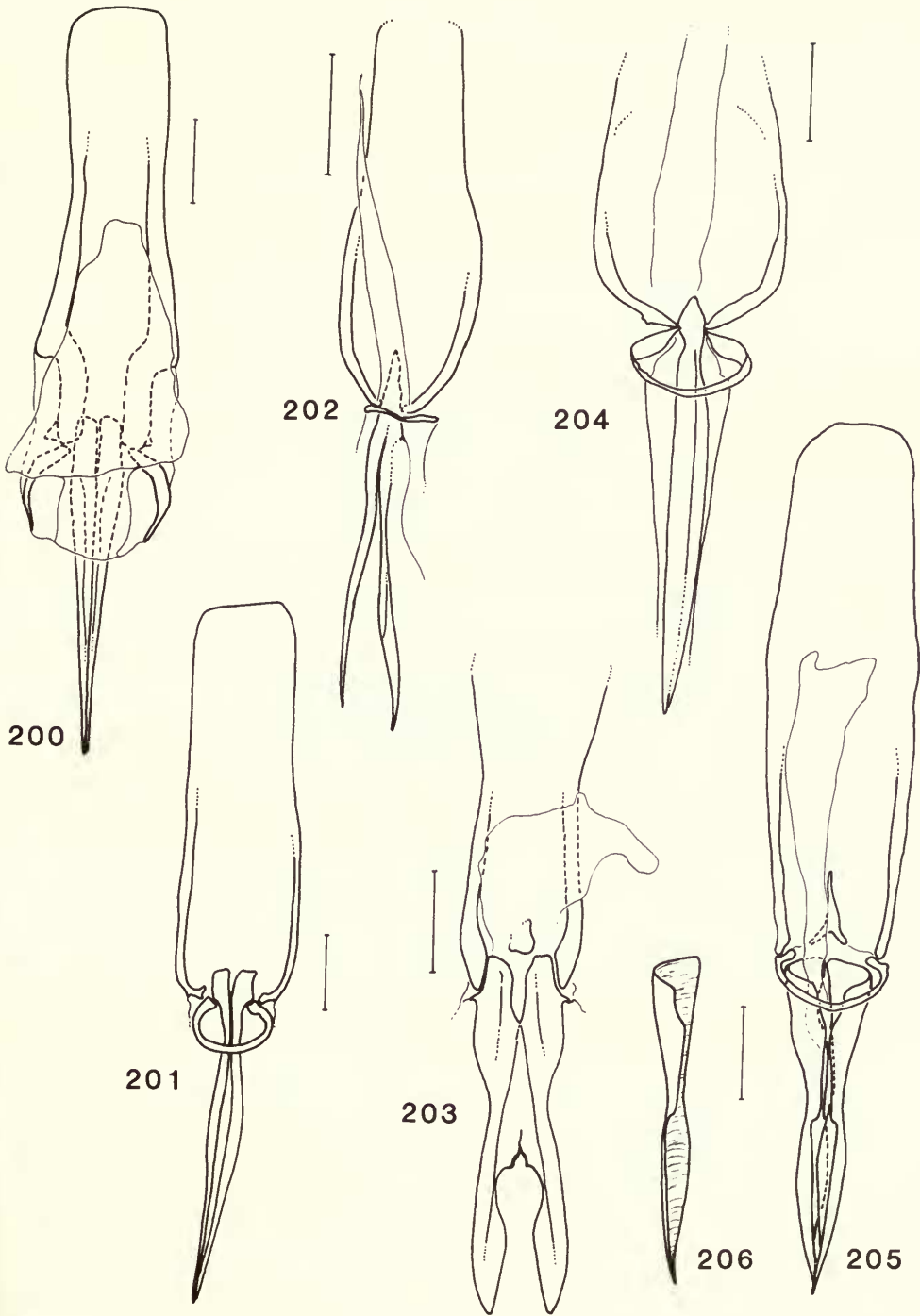
SPECIES INCLUDED

calogaleus (Bedford, 1928) (14 ♂, 24 ♀)

congoensis (Emerson & Price, 1967) **comb. n.** from *Suricatoecus* (23 ♂, 31 ♀)

cynictis (Bedford, 1938) (13 ♂, 19 ♀)

genettae (Fresca, 1924)



Figs 200–206 *Felicola* species, ♂ genitalia. 200, *F. (Suricatoecus) acutirostris*. 201, *F. (S.) vulpis*. 202, *F. (F.) liberiae*. 203, *F. (F.) minimus*, parameres displaced slightly apart. 204, *F. (F.) subrostratus*. 205, *F. (S.) decipiens*. 206, *F. (S.) decipiens*, detail of paramere.

- helogale* Bedford, 1932, **comb. rev.** from *Suricatoecus* (3 ♂, 7 ♀)
helogaloidis (Werneck, 1948) **comb. n.** from *Suricatoecus*
hopkinsi Bedford, 1936 **comb. rev.** from *Suricatoecus* (2 ♂, 1 ♀)
inaequalis (Piaget, 1880) (10 ♂, 19 ♀)
liberiae Emerson & Price, 1972 (7 ♂, 3 ♀)
minimus Werneck, 1948 (15 ♂, 28 ♀)
occidentalis (Emerson & Price, 1981) **comb. n.** from *Suricatoecus* (4 ♂, 5 ♀)
rahmi Emerson & Stojanovitch, 1966 (9 ♂, 16 ♀)
robertsi Hopkins, 1944 (8 ♂, 15 ♀)
rohani Werneck, 1956 (68 ♂, 62 ♀)
setosus Bedford, 1932 (14 ♂, 18 ♀)
subrostratus (Burmeister, 1838) (103 ♂, 120 ♀)
viverriculae (Stobbe, 1913) **comb. n.** from *Parafelicola* (21 ♂, 26 ♀; 6 ♂, 6 ♀ of undescribed sister-species)
zeylonicus Bedford, 1936 (6 ♂, 7 ♀)

Subgenus **SURICATOECUS** Bedford **stat. n.**

(Figs 176–178, 186–189, 194, 195, 200, 201, 205, 206)

Suricatoecus Bedford, 1932a: 354. Type-species: *Trichodectes cooleyi* Bedford, by monotypy.
Eichlerella Conci, 1942: 140. Type-species: *Trichodectes vulpis* Denny, by original designation. [Synonymy by Werneck, 1948: 172.]

DESCRIPTION. Preantennal portion of head with outline narrowly triangular or broadly rounded. Male scape not, or very slightly, expanded; male flagellum with 'teeth' absent or, if present, numbering one or three and basally articulated.

Abdominal spiracles absent, or present on segment III or segments III–V. Abdominal setae very short, of moderate length, or long and fine. Tergal and sternal sclerites generally present on abdomen, though less clear on posterior segments; male terga never with posterior sclerites.

Gonapophyses with rounded or rectangular lobe on ventral margin; spur present.

Everted portion of endophallus never sclerotised.

HOSTS. Canidae and Herpestidae (Carnivora).

COMMENTS. *Suricatoecus* has been treated not only as a genus, but also as a synonym and a subgenus of *Felicola* (Bedford, 1936 and Hopkins, 1949 respectively); a more complete history of the variations in status of *Suricatoecus* and of *Eichlerella* is provided in Table 5. Eichler (1963) included the manuscript name *Felicomorpha* in his catalogue, without providing any further details, the name therefore being a nomen nudum. In an earlier, unpublished work, Eichler had attributed this name to Kéler m.s., and noted the type-species, which is a junior synonym of *T. vulpis* Denny. *Felicomorpha* is, however, not an available name.

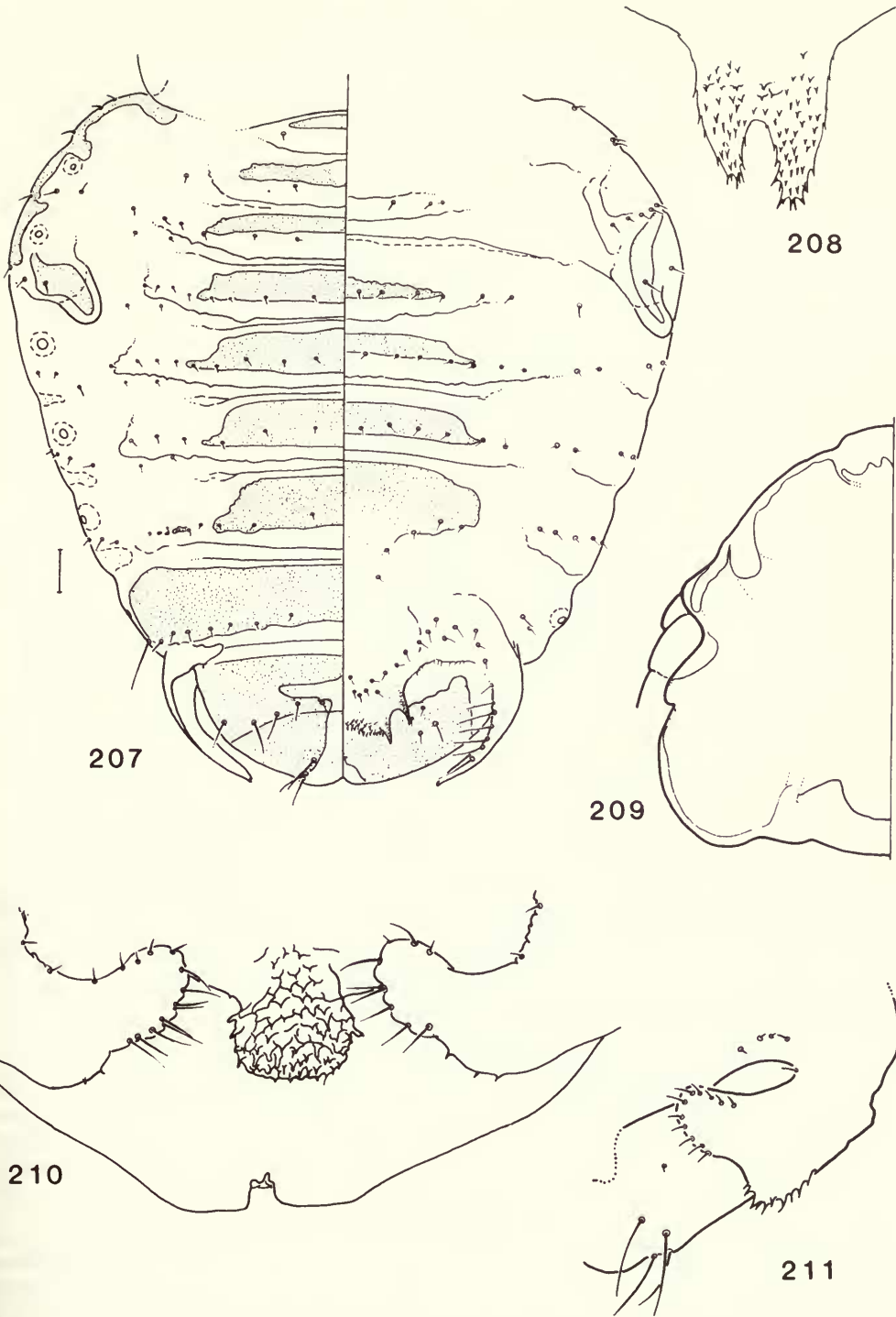
SPECIES INCLUDED

- acutirostris* (Stobbe, 1913) [treated as *Felicola* s. str. by previous authors] (2 ♂, 2 ♀)
bedfordi Hopkins, 1942 [treated as *Felicola* s. str. by previous authors] (4 ♂, 11 ♀)
cooleyi (Bedford, 1929) **comb. n.** from *Suricatoecus* (30 ♂, 28 ♀)
decipiens Hopkins, 1941 **comb. rev.** from *Suricatoecus* (9 ♂, 9 ♀)
fahrenheitzi (Werneck, 1948) **comb. n.** from *Suricatoecus* (16 ♂, 16 ♀)
fennecus (Emerson & Price, 1981) **comb. n.** from *Suricatoecus*
guinlei (Werneck, 1948) **comb. n.** from *Suricatoecus* (4 ♂, 10 ♀)
macrurus Werneck, 1948 [treated as *Felicola* s. str. by previous authors] (23 ♂, 19 ♀)
pygidialis Werneck, 1948 [treated as *Felicola* s. str. by previous authors] (36 ♂, 41 ♀)
quadratriceps (Chapman, 1897) **comb. n.** from *Suricatoecus* (5 ♂, 9 ♀)
vulpis (Denny, 1842) **comb. n.** from *Suricatoecus* (18 ♂, 25 ♀)

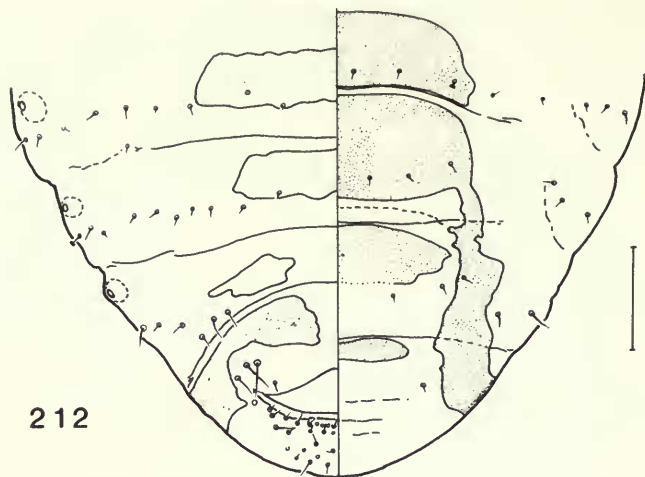
Genus **LORISICOLA** Bedford

The genus *Lorisicola* comprises two subgenera.

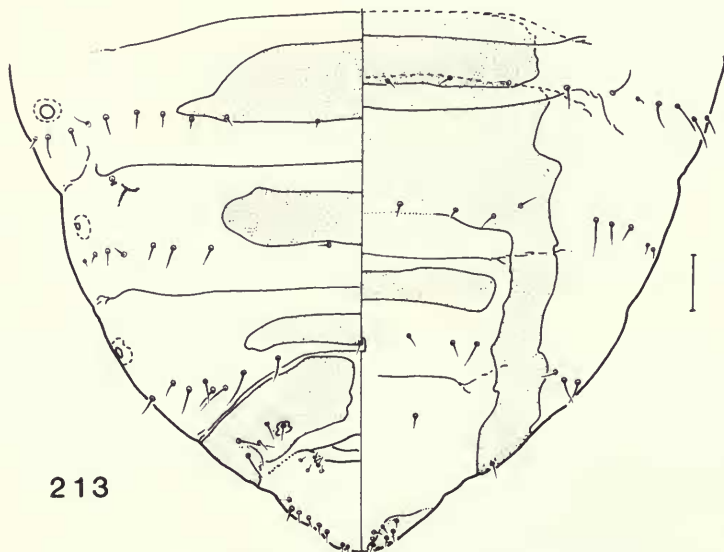
DESCRIPTION. Anterior of head with osculum present or absent*; dorsal preantennal sulcus present or absent; clypeal marginal carina broadened medially, median sclerite variable*; anterolateral margin of



Figs 207–211 *Loricicola* species. 207, *L. (L.) mjoebergi*, ♀ abdomen. 208, *L. (Paradoxuroecus) bengalensis*, ♀ subgenital lobe, ventral. 209, *L. (P.) africanus*, ♀ head, dorsal. 210, *L. (L.) spenceri*, ♀ terminalia, ventral, setae omitted apart from on gonapophyses. 211, *L. (L.) felis*, ♀ gonapophysis, ventral.



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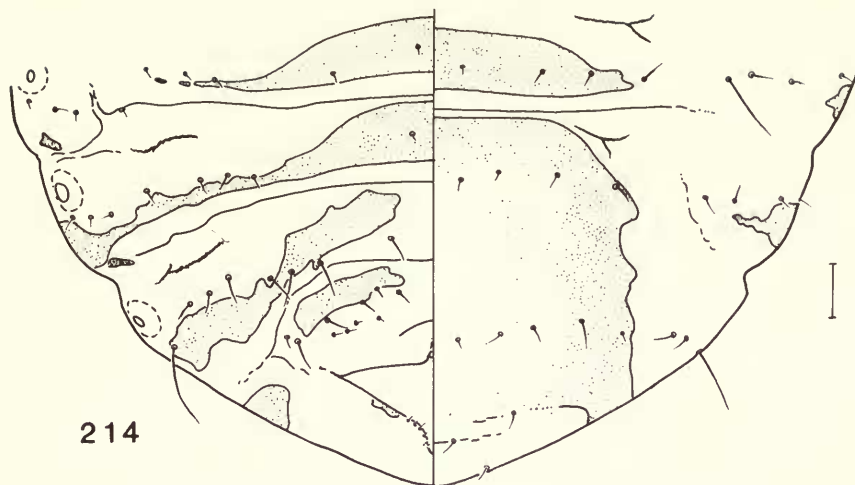
213

Figs 212, 213 *Lorisicola* (L.) species, ♂ terminalia. 212, *L. (L.) similis*. 213, *L. (L.) spenceri*.

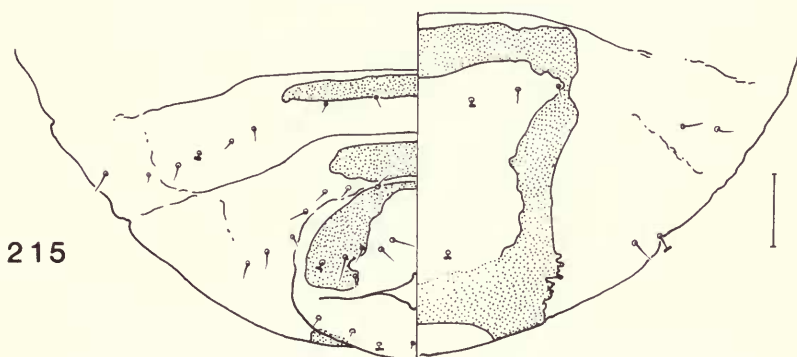
head sinuate or convex; preantennal portion of head of variable length, outline more or less broadly triangular or rounded, sometimes, if osculum absent, convexly produced anteriorly*. Temple margin convex, rectangular, or slightly produced laterally*. Male scape expanded or only slightly expanded, with longitudinal setal row present and comprising at least two setae*; male and female flagellomeres fused; male flagellum with one or two basally-articulated teeth*. Dorsum of head with setae short or of moderate length, sparse. Sitophore sclerite unmodified.

Thorax with dorsal setae short or of moderate length* though frequently short and stout on postero-lateral angles of pterothorax, not present on disc or medially posteriorly on prothorax or pterothorax.

Abdomen oval or elongate, male segment IX not produced greatly. Abdominal spiracles absent, or present on segments III–VI or III–VIII; posterior two pairs of spiracles, if six pairs present, sometimes very small and possibly non-functional*. Abdominal setae short or very short, frequently sparse dorsally; abdominal pleurum III frequently with posterior setal row comprising stout, conical setae (Fig. 218); anterior setae absent except on pleurum II; postero-lateral setae present or absent, sometimes numbering more than one per site* (Fig. 207). Pleural projections present dorsally and sometimes ventrally on pleurum IV, sclerotised or unsclerotised. Abdominal sclerotisation variable; sterna with sclerites absent



214



215

Figs 214, 215 *Loricicola* species, ♂ terminalia. 214, *L. (L.) mjoebergi*. 215, *L. (Paradoxuroecus) laticeps*.

except for subgenital plate (in male), or present on more posterior segments (VII, VI+VII, V-VII, IV-VII or III-VII); terga with sclerites on I-VIII, II-VIII, III-VIII or IV-VIII; pleura with sclerites on at least II, sometimes also on III and IV; male terga with anterior and posterior sclerites present on at least terga IV-VII, or posterior sclerites not present*.

Gonapophyses with ventral marginal non-tuberculate setae; rounded or rectangular lobe present or absent on ventral margin*; apical spur present or absent*. Gonapophyses meet ventral vulval margin acutely, not linked by sclerotised band. Ventral vulval margin not sclerotised; straight or concave, with chord less than 90 degrees to long axis of abdomen; subgenital lobe present, ventral surface more or less covered in overlapping scales*.

Male subgenital plate with sternites VII, VIII and IX present and fused to s.g.p.r., VII and VIII fused to s.g.p.r. and IX absent, or VII fused to s.g.p.r. and VIII and IX absent or present but not fused to s.g.p.r.*. Pseudostyli absent. Male genital opening postero-dorsal or dorsal; male segment IX lying dorsally on abdomen. Parameres short, broad, sometimes fused. Basiparameral sclerites present or absent*. Mesomeres present, fused; median extension present or absent*; mesomeres extending basally between b.a.l.s. to contact parameres, or terminating exteriorly to b.a.l.s.*. Male genitalia depicted in Figs 219-226.

Hosts. Felidae, Herpestidae and Viverridae (Carnivora) and Loriscidae (Primates).

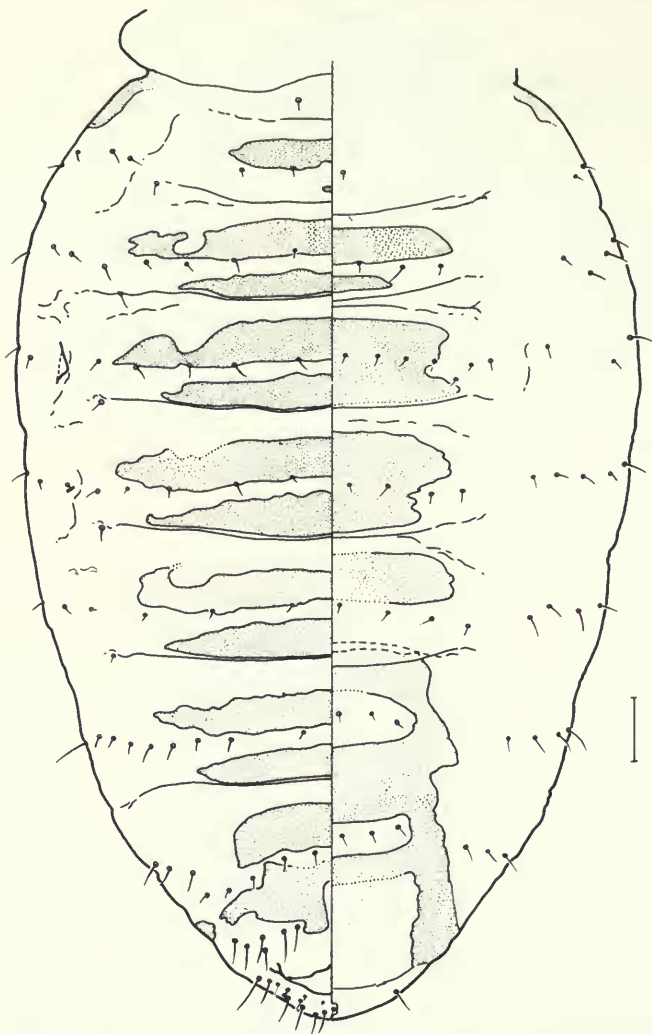


Fig. 216 *Loricicola (Paradoxuroecus) acuticeps*, ♂ abdomen.

Subgenus **LORISICOLA** Bedford

(Figs 207, 210–214, 219, 220)

Loricicola Bedford, 1936: 51. Type-species: *Trichodectes mjoergei* Stobbe, by original designation.

DESCRIPTION. Anterior of head with osculum present; clypeal marginal carina broadened medially to form rectangular or W-shaped sclerite, or broadened slightly to either side of osculum, very lightly sclerotised posterior to osculum. Temple margin rectangular or slightly produced laterally. Male scape expanded or only slightly expanded, with setal row comprising two setae; male flagellum with basally-articulated 'teeth' on projection.

Abdominal spiracles absent, or present on segments III–VIII; posterior two pairs of spiracles, if six pairs present, sometimes very small and possibly non-functional. Males with posterior tergal sclerites absent.

Gonapophyses with rounded lobe, or lobe absent (Fig. 207); apical spur present or absent (Fig. 211). Subgenital lobe covered in overlapping pointed scales (Fig. 210) or spines (Fig. 207).

Male subgenital plate with sternites VII, VIII and IX present and fused to s.g.p.r. (Fig. 214), or with sternite VII fused to s.g.p.r. and VIII and IX present but not fused to s.g.p.r. (Fig. 212), or of the latter form but lacking sternite IX (Fig. 213), or lacking VIII and IX but VII very broad. Basiparameral sclerites absent. Mesomeres fused, with median extension. Mesomeres extending basally between b.a.l.s. to

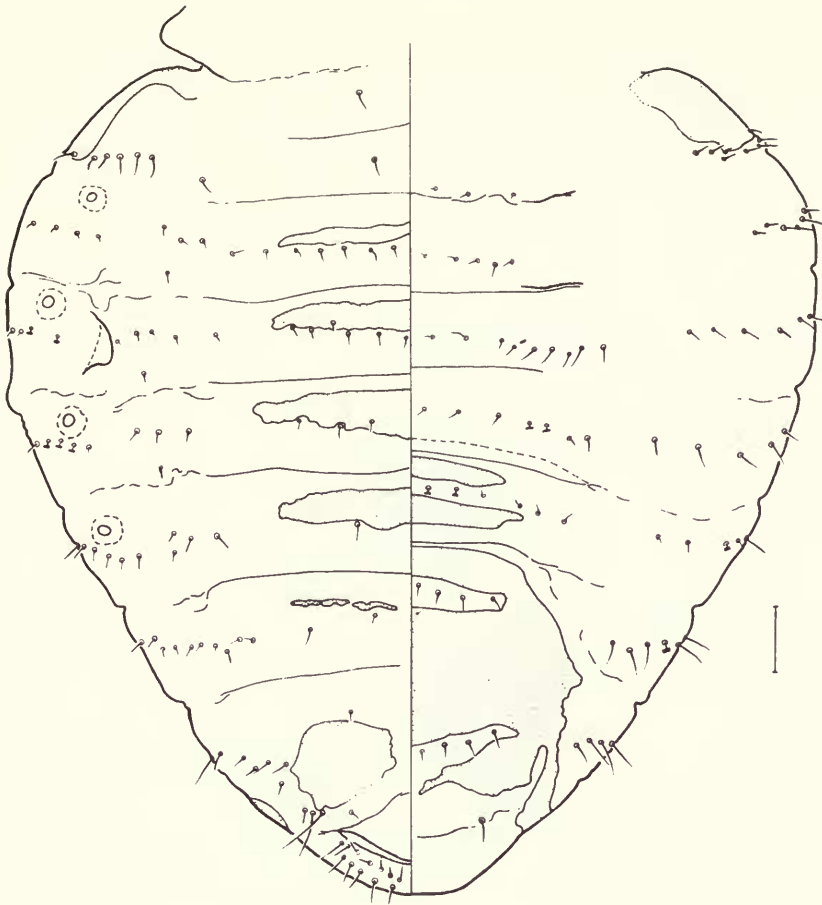


Fig. 217 *Lorisicola (Paradoxuroecus) bengalensis*, ♂ abdomen.

contact parameres (Fig. 222), terminating exteriorly to b.a.l.s. (Fig. 220), or extending anterior to posterior end of b.a.l.s. and abruptly reversing, lying ventrally to b.a.l.s., though reversed portion is difficult to see (Fig. 219).

Hosts. Felidae and Viverridae (Carnivora) and Loriscidae (Primates).

COMMENTS. The original spelling *mjöbergi* is emended here to *mjoebergi* in accordance with Article 32(d)(i) of the *International Code of Zoological Nomenclature* (1984).

SPECIES INCLUDED

- americanus* (Emerson & Price, 1983) **comb. n.** from *Felicola*
- braziliensis* (Emerson & Price, 1983) **comb. n.** from *Felicola*
- caffra* (Bedford, 1919) **comb. n.** from *Felicola* (1 ♂, 1 ♀)
- felis* (Werneck, 1934) **comb. n.** from *Felicola* (1 ♂, 1 ♀)
- hercynianus* (Kéler, 1957) **comb. n.** from *Felicola* (6 ♂, 6 ♀)
- malaysianus* (Werneck, 1948) **comb. n.** from *Trichodectes* (4 ♂, 5 ♀)
- mjoebergi* (Stobbe, 1913) (c.100 ♂, c.100 ♀)
- neofelis* (Emerson & Price, 1983) **comb. n.** from *Felicola*
- siamensis* (Emerson, 1964) **comb. n.** from *Felicola* (5 ♂, 2 ♀)
- similis* (Emerson & Price, 1983) **comb. n.** from *Felicola* (1 ♂, 1 ♀)
- spenceri* (Hopkins, 1960) **comb. n.** from *Felicola* (8 ♂, 5 ♀)
- sudamericanus* (Emerson & Price, 1983) **comb. n.** from *Felicola*

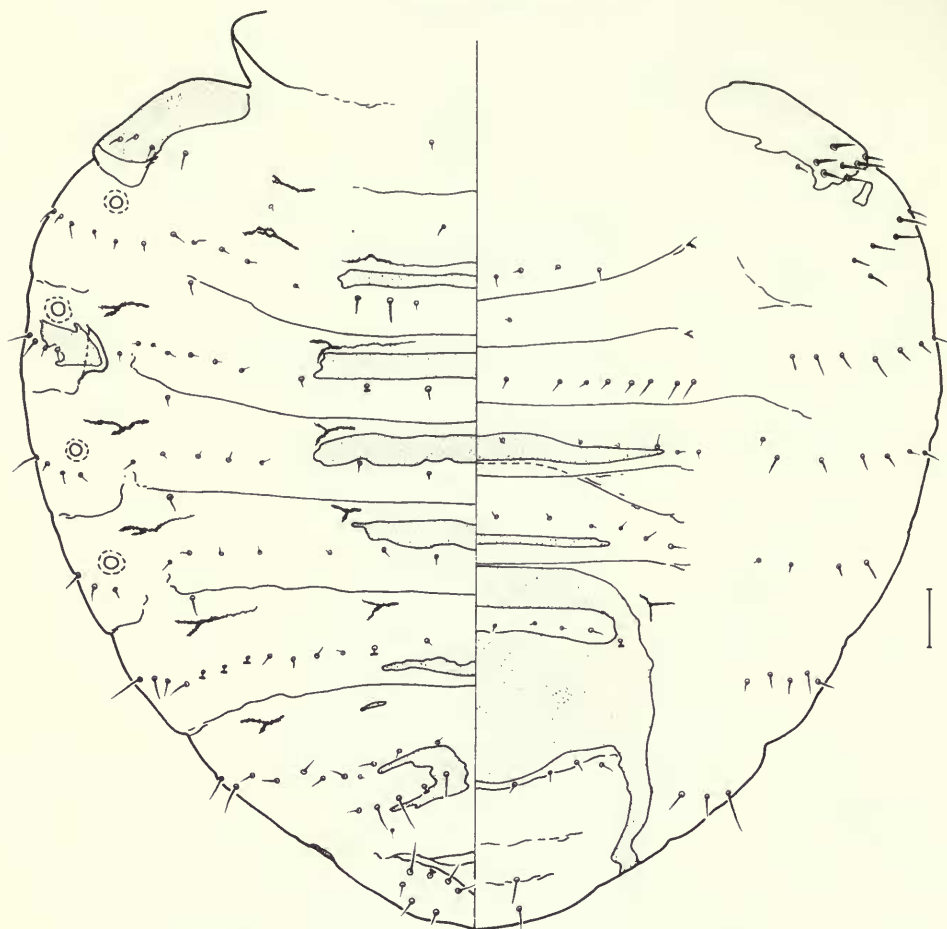


Fig. 218 *Loricicola (Paradoxuroecus) juccii*, ♂ abdomen.

Subgenus **PARADOXUROECUS** Conci gen. rev., stat. n.

(Figs 208, 209, 215–218, 221–226)

Paradoxuroecus Conci, 1942: 141. Type-species: *Paradoxuroecus juccii* Conci, by original designation.

Parafelicola Werneck, 1948: 226. Type-species: *Trichodectes acuticeps* Neumann, by original designation.

Syn. n.

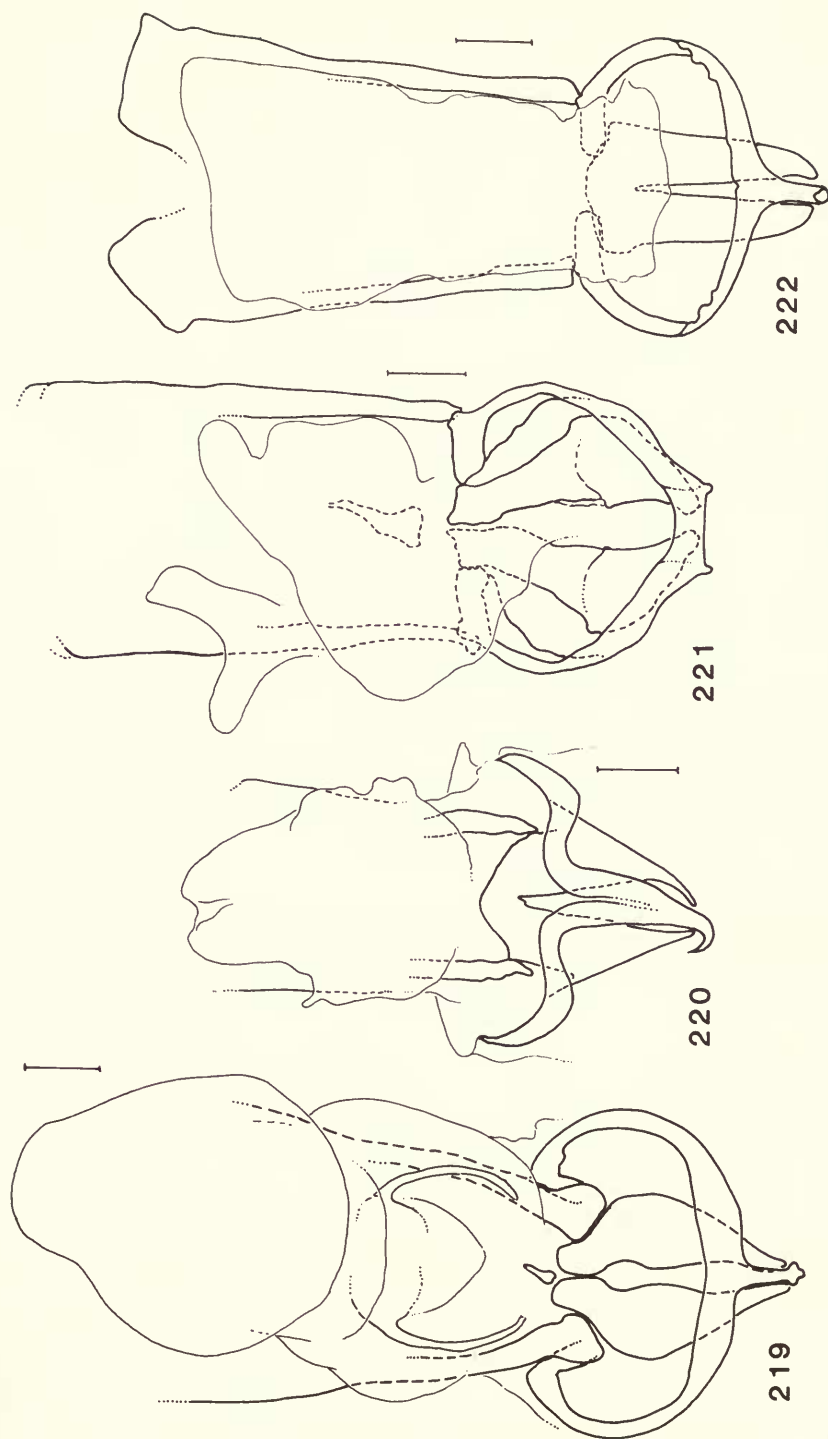
Neofelicola Werneck, 1948: 235. Type-species: *Neofelicola aspidorhynchus* Werneck, by original designation. **Syn. n.**

DESCRIPTION. Anterior of head with osculum present, in which case clypeal marginal carina broadened slightly to either side of osculum and very lightly sclerotised posterior to osculum, or osculum absent, in which case clypeal marginal carina broadened medially to form posteriorly-convex or straight heavily sclerotised bar (Fig. 209); outline of preantennal portion of head more or less broadly rounded or triangular, sometimes, if osculum absent, convexly produced anteriorly (Fig. 209). Temple margin convex or rectangular. Male scape expanded or only slightly expanded, with longitudinal setal row comprising at least three setae; male flagellum with two basally-articulated 'teeth', only rarely on projection.

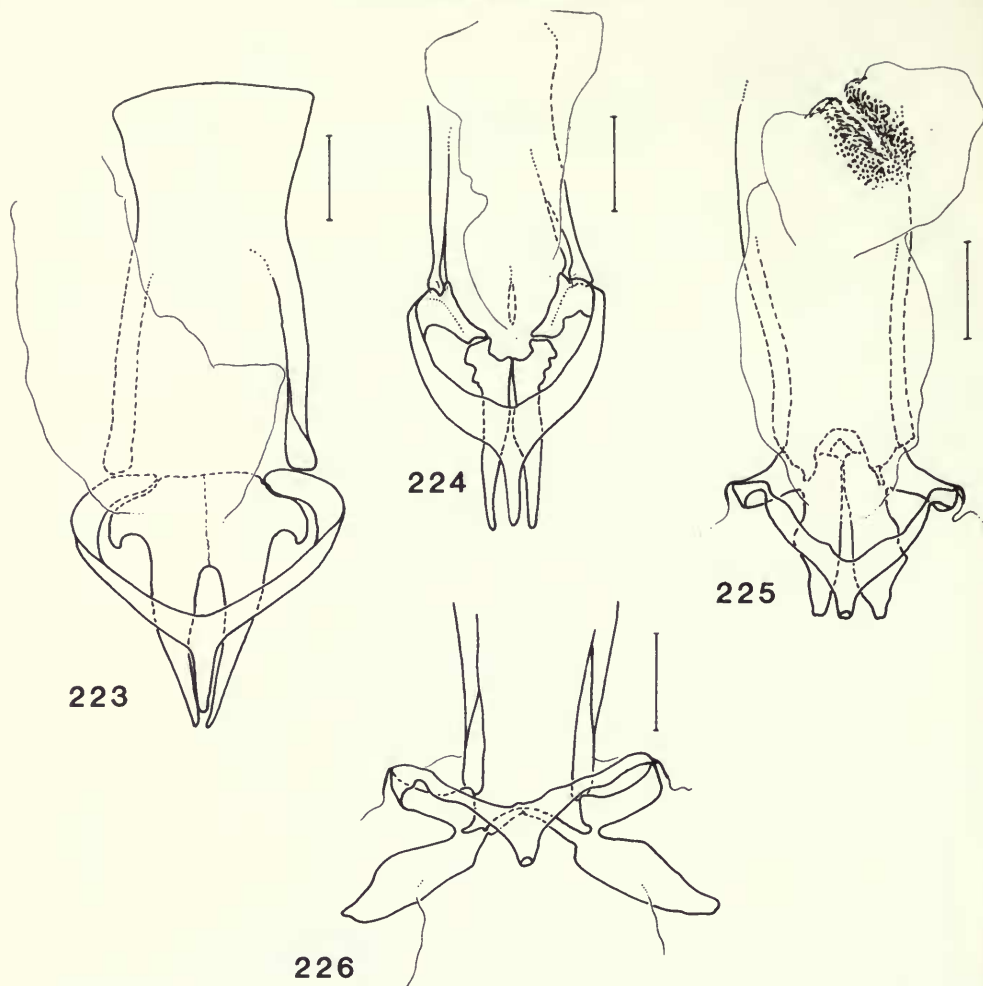
Thorax with dorsal setae short.

Abdominal spiracles absent, or present on segments III–VI. Postero-lateral setae present or absent, but never numbering more than one per site if present. Males with posterior tergal sclerites absent, or anterior and posterior sclerites present on at least terga IV–VII.

Gonapophyses with lobe present, rounded or rectangular; apical spur present. Subgenital lobe bilobate, with scales modified into short spines in some cases, though spines may be sparse (Fig. 208).



Figs 219-222 *Loricicola* species, ♂ genitalia. 219, *L. (L.) mjoeborgi*. 220, *L. (L.) malaysianus*. 221, *L. (Paradoxuroecus) laticeps*. 222, *L. (P.) spenceri*.



Figs 223–226 *Lorisicola* (*Paradoxuroecus*) species, ♂ genitalia. 223, *L. (P.) juccii*. 224, *L. (P.) bengalensis*. 225, *L. (P.) acuticeps*. 226, *L. (P.) acuticeps*, endophallus everted.

Male subgenital plate with sternites VII, VIII and IX present and fused to s.g.p.r. (Fig. 216), VII and IX present and fused to s.g.p.r. but VIII absent (Fig. 215), or VII and VIII present and fused to s.g.p.r. but IX absent (Figs 217, 218). Parameres short, broad, not fused together (see second paragraph under 'comments' below), but may be very closely associated (Figs 223, 224). Basiparameral sclerites present (Fig. 225) or absent. Mesomeres fused apically with median extension present or, if absent, arch with two apical nipples (Fig. 221); mesomer arch sometimes with lateral double flexion (Fig. 225); mesomeres extending basally between b.a.l.s. to contact parameres, sometimes sharply recurved posteriorly between b.a.l.s. (Fig. 224). Endophallus frequently with spicular collar, sometimes V-shaped, around gonopore (Fig. 225).

Hosts. Herpestidae and Viverridae (Carnivora).

COMMENTS. *Paradoxuroecus* has been considered by most authors, following Werneck (1948), to be a synonym of *Felicola*; it is here recalled from synonymy and placed as a subgenus of *Lorisicola*. *Neofelicola* and *Parafelicola* were both considered by Hopkins (1949) to be subgenera of *Felicola*. A more complete history of the variations in the status of *Paradoxuroecus*, *Neofelicola* and *Parafelicola* is presented in Table 5.

Werneck (1948) figured the parameres of *aspidorhynchus*, *sumatrensis* and *juccii* as fused together; examination of the type-material of the first two species and of numerous specimens of the last has revealed that this is not the case, although in *L. juccii* the parameres are very closely associated with each other.

Loricicola (Paradoxuroecus) bengalensis (Werneck, 1948) was described in *Neofelicola* from three females, the male being unknown. These females were taken from a museum skin of *Paradoxurus hermaphroditus canus* Miller, which was itself collected in Thailand. Female lice subsequently collected from *P. hermaphroditus* subsp. in Thailand agree with Werneck's (1948) description of *N. bengalensis*. Emerson (1965) describes the male of *bengalensis*, collected from the type host in Thailand, and distinguishes a new species, *N. philippinensis*, collected from *Paradoxurus philippinensis*.

Numerous specimens of lice from a number of subspecies of *Paradoxurus hermaphroditus* have been examined during the course of this study, and it has become apparent that lice of two clades are present: the *Felicola (F.) zeylonicus-viverriculae* clade and the *Loricicola (P.) philippinensis-juccii* clade.

These clades may be distinguished by the following characters.

F. (F.) zeylonicus-viverriculae clade – Three pairs of abdominal spiracles; male flagellum with 'teeth' not basally articulated; parameres long, slender, extending anteriorly between b.a.l.s.; mesomeres not basally extending between b.a.l.s.; mesomeral arch lacking median extension; female subgenital lobe broad, smooth ventrally, with long, flattened marginal spines.

L. (P.) philippinensis-juccii clade – Four pairs of abdominal spiracles; male flagellum with 'teeth' basally articulated; parameres short, broad, closely-associated with one another but not fused, not extending between b.a.l.s., if reaching them; mesomeres basally extending between b.a.l.s. to contact parameres; mesomeral arch with median extension; female subgenital lobe narrow, apically bilobate, covered ventrally with small pointed scales, lacking marginal spines.

The female described as *N. bengalensis* by Werneck (1948) is, by the structure of the subgenital lobe and the number of abdominal spiracles, a member of the *L. (P.) philippinensis-juccii* clade, as are both male and female of *N. philippinensis* as described by Emerson (1965). The male described by Emerson (1965) as *N. bengalensis* is, however, a member of the *F. (F.) zeylonicus-viverriculae* clade and therefore not the true male of *N. bengalensis*. Female lice of the latter clade are now known from *Paradoxurus hermaphroditus* subsp., as are males of the former.

The male of *L. bengalensis* has genitalia indistinguishable from those of *L. philippinensis*. Emerson (1965) distinguishes *L. philippinensis* from *L. bengalensis* by the male genitalia, the greater number of sternal and tergal setae in both sexes of the former, and the greater number of vulval setae in the former. The characteristics of the male genitalia, as stated above, are the same in the two species. Study of the large sample of specimens now available indicates that the vulval setal number of *L. philippinensis* is not outside the range of *L. bengalensis*. The tergal and sternal setae in the males are the same, as are the sternal setae in the females. The tergal setae of the female paratype of *L. philippinensis* in the British Museum (Natural History) collection are the same as those of *L. bengalensis*, but do not agree with the figure in Emerson (1965), where far more setae are depicted. The host species *Paradoxurus philippinensis* is at best a subspecies of *P. hermaphroditus*, and all other subspecies appear to harbour *L. bengalensis*. *L. philippinensis* (Emerson) is consequently provisionally synonymised with *L. bengalensis* (Werneck), subject to examination of the female allotype of *philippinensis*.

SPECIES INCLUDED

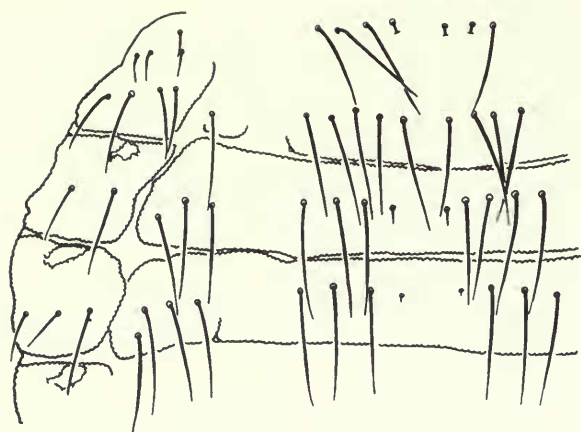
- acuticeps* (Neumann, 1902) **comb. n.** from *Parafelicola* (28 ♂, 34 ♀)
- africanus* (Emerson & Price, 1966) **comb. n.** from *Parafelicola* (15 ♂, 7 ♀)
- aspidorhynchus* (Werneck, 1948) **comb. n.** from *Neofelicola* (6 ♂, 7 ♀)
- bengalensis* (Werneck, 1948) **comb. n.** from *Neofelicola* (26 ♂, 59 ♀)
- juccii* Conci, 1942 **comb. n.** from *Felicola* (82 ♂, 81 ♀)
- laticeps* (Werneck, 1942) **comb. n.** from *Suricatoecus* (10 ♂, 13 ♀)
- lenicornis* (Werneck, 1948) **comb. n.** from *Parafelicola* (9 ♂, 22 ♀)
- mungos* (Stobbe, 1913) **comb. n.** from *Suricatoecus* (1 ♂, 3 ♀)
- neoafricanus* (Emerson & Price, 1968) **comb. n.** from *Parafelicola* (holotype ♂, 4 ♀)
- paralaticeps* (Werneck, 1948) **comb. n.** from *Suricatoecus* (1 ♂, 4 ♀)
- philippinensis* (Emerson, 1965) **comb. n.** from *Neofelicola* (5 ♂, 5 ♀)
- sumatrensis* (Werneck, 1948) **comb. n.** from *Neofelicola* (4 ♂, 4 ♀)
- wernecki* (Hopkins, 1941) **comb. n.** from *Parafelicola* (7 ♂, 11 ♀)

NEOTRICHODECTINAE subfam. n.

Type-genus: *Neotrichodectes* Ewing

Genus **NEOTRICHODECTES** Ewing

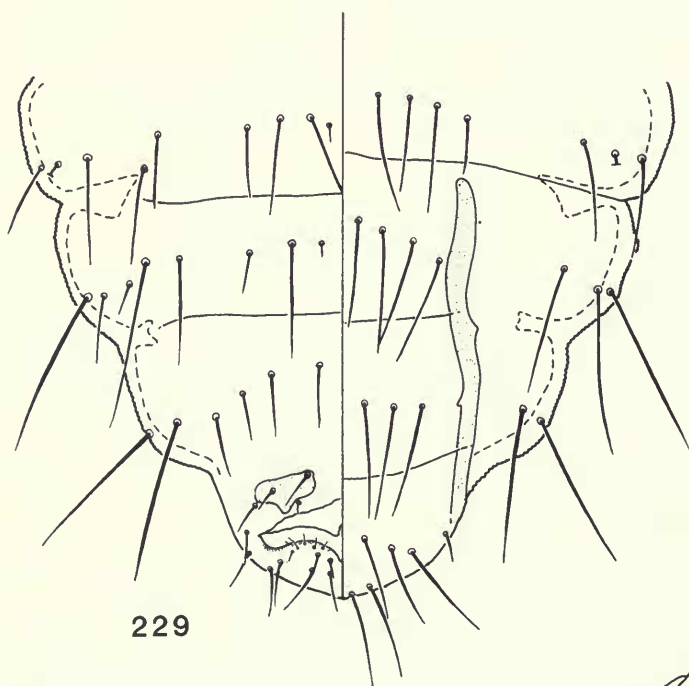
The genus *Neotrichodectes* comprises five subgenera.



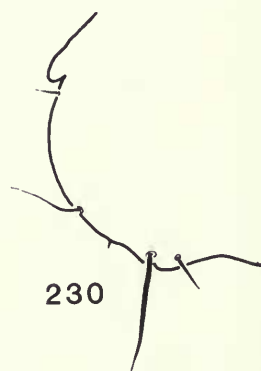
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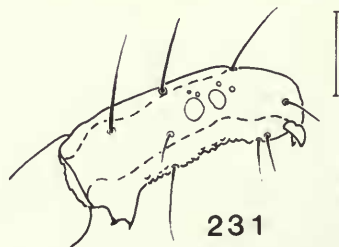
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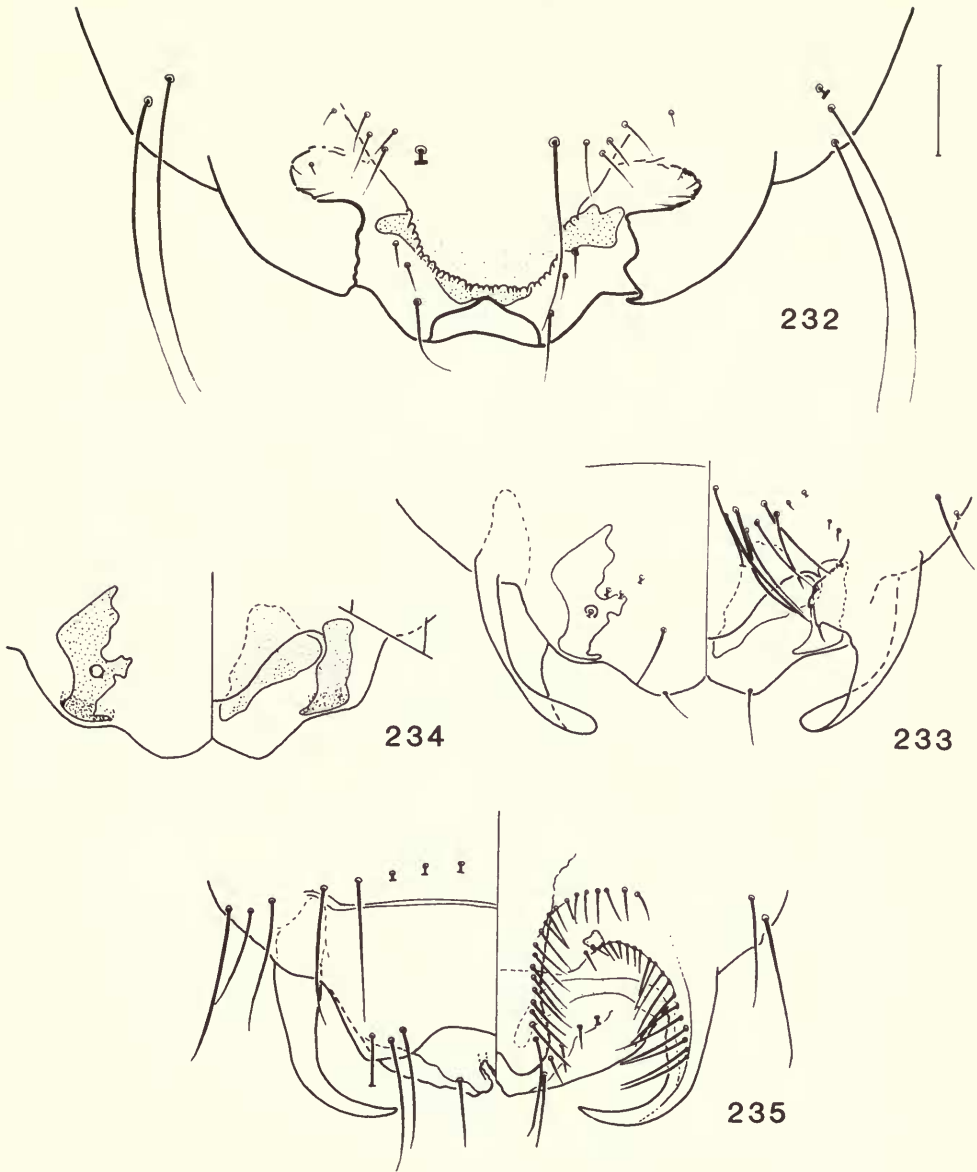
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231

Figs 227–231 *Neotrichodectes* species. 227, *N. barbarae*, ♂ anterior abdominal segments, dorsal. 228, *N. mephitidis*, ♀ abdominal pleura II and III, dorsal. 229, *N. mephitidis*, ♂ terminalia. 230, *N. barbarae*, ♂ temple margin. 231, *N. semistriatus*, ♂ flagellum.

DESCRIPTION. Anterior of head with osculum present, sometimes very shallow*; dorsal preantennal sulcus present, not always clear; clypeal marginal carina broadened medially into dorsal sclerite of variable form* which is always more heavily sclerotised laterally (dorsal to margin of clypeus and pulvinus) than medially; antero-lateral margin of head convex, straight or sinuate*; preantennal portion of head short or longer, sometimes as long as postantennal portion*, outline broadly rounded or triangular*. Temple margin broadly convex. Male scape expanded, with longitudinal setal row present and comprising at least four setae; flagellomeres fused in males and females; male flagellum with two or more basally-articulated 'teeth'

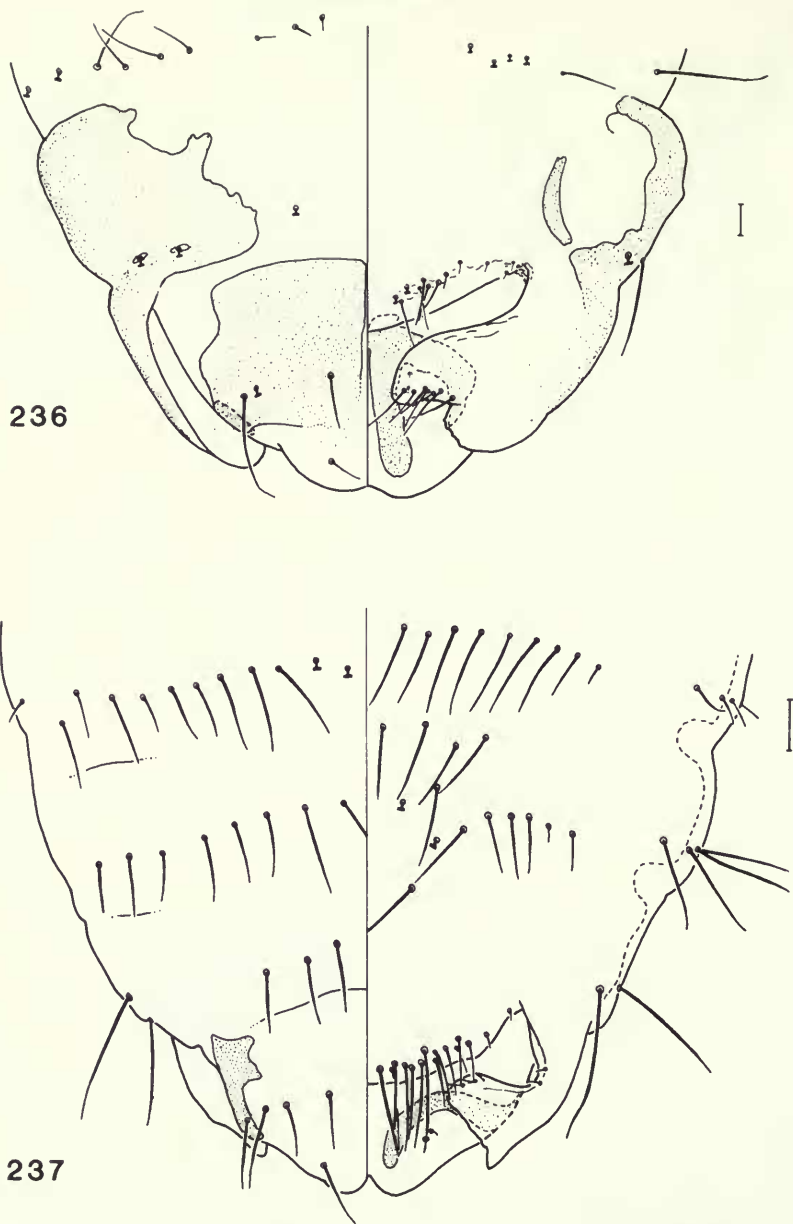


Figs 232–235 *Neotrichodectes* species, ♀ terminalia. 232, *N. mephitidis*, ventral. 233, *N. chilensis*, showing setal distribution. 234, *N. chilensis*, showing sclerites. 235, *N. barbarae*.

distally, and with basal toothed or rough projection sometimes present* (Fig. 231); female pedicel lacking membranous projection. Dorsum of head with most setae short or of moderate length, more or less sparse, sometimes with long seta on posterior margin of temple* (Fig. 230). Sitophore sclerite unmodified.

Thorax with dorsal setae long or of moderate length* though frequently short and spine-like on postero-lateral angles of prothorax and pterothorax; posterior margin of pronotum with four setae and wide median gap, posterior of pterothorax dorsally with setae more abundant, marginal or submarginal, median gap present or absent.

Abdomen broadly rounded, not greatly projecting posteriad in male (Fig. 229). Abdominal spiracles absent. Abdominal setae generally abundant, as long as segment or sparse, shorter, with long setae present only on posterior pleura*; terga, especially of males, with median and lateral setal groups distinct, though median groups generally united; male terga II–VI with median two setae much smaller than other setae in the row, sometimes separated by one or more longer setae (Fig. 229); anterior setae present on

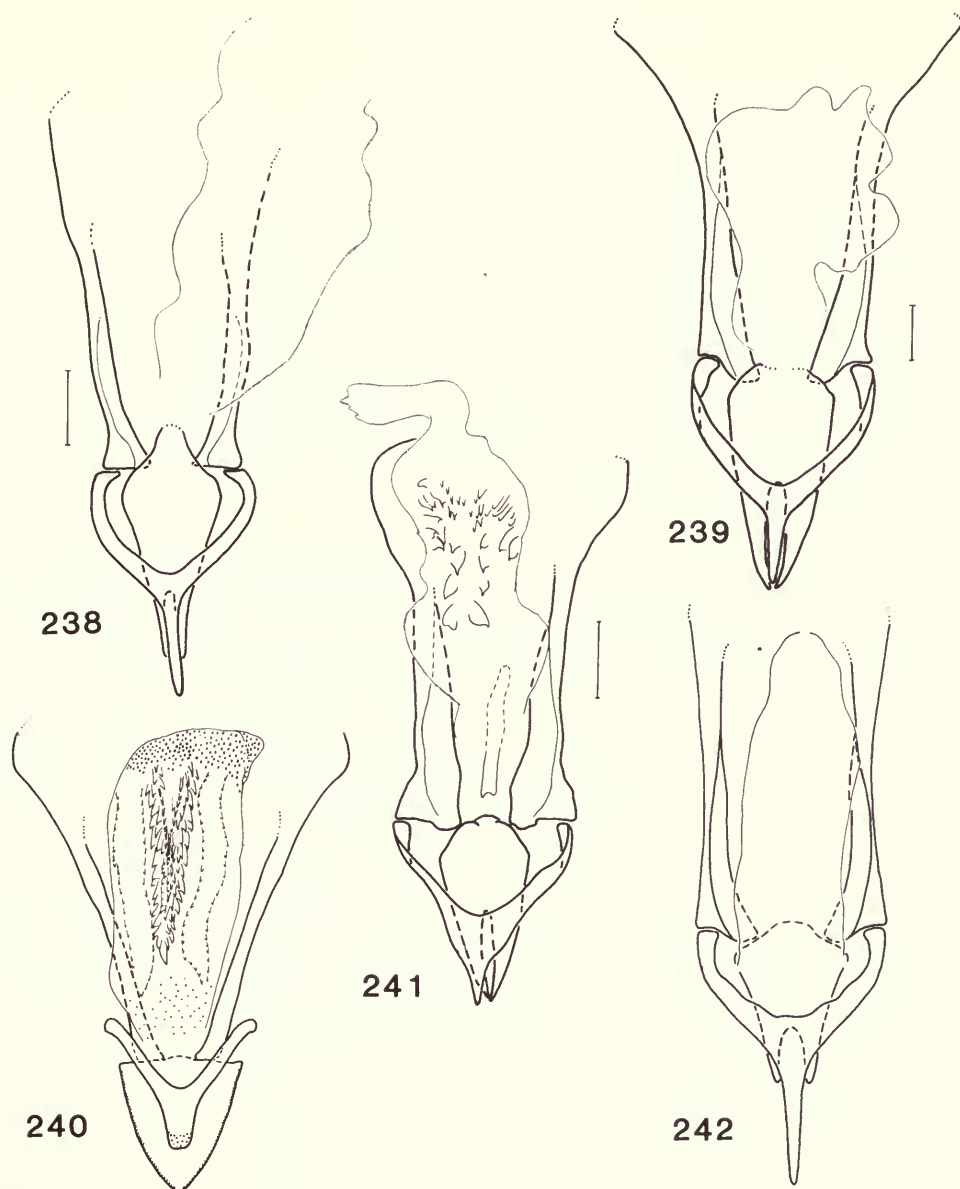


Figs 236, 237 *Neotrichodectes* species, ♀ terminalia. 236, *N. gastrodes*. 237, *N. pallidus*.

pleura II and III only; postero-lateral setae presumed absent, though possibly present as the most lateral seta of lateral group, which is frequently situated more posteriorly than other setae. Abdominal pleura lacking projections, except for small sclerotised or unsclerotised projection dorsally on pleurum III of female *N. mephitidis*. Abdominal terga and sterna lacking sclerites, except for lateral rods of subgenital plate in male and, sometimes, tergite IX in female; abdominal pleura usually unsclerotised, sometimes with sclerites on pleura II, III, IV and, in females, VIII*.

Gonapophyses with or without lobe on ventral margin, very variable*. Gonapophyses meet ventral vulval margin smoothly or acutely, but not linked by sclerotised band. Ventral vulval margin not sclerotised; generally convex medially*, subgenital lobe present or absent*. Common oviduct not notably striate (cf. *Geomydoecus*).

Male subgenital plate with only s.g.p.r. present (Fig. 229). Pseudostyli absent. Male genital opening



Figs 238–242 *Neotrichodectes* species, ♂ genitalia. 238, *N. (Neotrichodectes) mephitidis*. 239, *N. (Nasuicola) pallidus*. 240, *N. (Trigonodectes) barbarae*. 241, *N. (Lakshminarayanaella) gastrosdes*. 242, *N. (Conepaticola) chilensis*.

dorsal. Parameres fused to form single plate with apex pointed or bifid*. Basiparameral sclerites absent. Mesomeres fused apically; mesomerar arch with median extension*; mesomeres basally abut postero-lateral projections of b.a.l.s. but do not contact parameral plate (Fig. 242), or contact neither b.a.l.s. nor parameral plate (Fig. 240).

HOSTS. Mustelidae and Procyonidae (Carnivora) and Bradypodidae (Edentata).

COMMENTS. *Neotrichodectes* has been considered a synonym and a subgenus of *Trichodectes* (by Hopkins, 1942 and Hopkins, 1949 respectively); a more complete history of the variations in status of *Neotrichodectes* is presented in Table 4.

Subgenus **NEOTRICHODECTES** Ewing

(Figs 228, 229, 232, 238)

Neotrichodectes Ewing, 1929: 194. Type-species: *Goniodes mephitidis* Packard, by original designation.

DESCRIPTION. Anterior of head with clypeal marginal carina broadened into dorsal sclerite which is more or less convex posteriorly, sometimes almost circular; preantennal portion of head sometimes as long as postantennal portion. Male flagellum with two basally-articulated 'teeth' distally, and with toothed projection sometimes present basally (Fig. 231). Temple with long seta present on posterior margin.

Thoracic and abdominal setae long, abundant. Abdominal pleura lacking projections, except for small sclerotised or unsclerotised projection dorsally on pleurum III of female *N. mephitidis* (Fig. 228). Abdomen lacking sternal, tergal and pleural sclerites, except for lateral rods of male subgenital plate.

Gonapophyses broad, membranous, with ventral marginal setae absent or, if present, basal only (Fig. 232); ventral lobe absent. Ventral vulval margin with lobe present though difficult to see; lobe serrate, at least along posterior margin (Fig. 232). Female genital chamber with dorsal wall bearing slanting scales laterally, lightly sclerotised and lacking scales or other decoration medially (anteriorly).

Parameral plate slender, apically bifid, with median basal extension reaching anteriorly between b.a.l.s. Mesomer arch with median extension pointed; mesomeres basally abut postero-lateral extensions of b.a.l.s. Male genitalia depicted in Fig. 238.

HOSTS. Mustelidae and Procyonidae (Carnivora).

COMMENTS. *Neotrichodectes* s. str. is most readily distinguished from other subgenera of *Neotrichodectes* by characters of the female terminalia: the retention of the plesiomorphic form of the gonapophyses (found also in *Geomydoecus*) and the apomorphic development of a membranous subgenital lobe (cf. the very different structure in *N. (Trigonodectes)*). Assignment of male insects to the subgenus relies on absence of the basal flagellar projection (a character-state reversal not undergone by the type-species of the subgenus), the presence of an anterior development of the parameral plate between the b.a.l.s., and the slenderness of that parameral plate in relation to its length. *Neotrichodectes wolffhuegeli* (Werneck) is known only from the male, although Werneck (1948) predicted that the female would be very similar to that of *N. chilensis* (placed in *N. (Conepaticola)* in this study), and so must be assigned to subgenus on the basis of male characters. *N. wolffhuegeli* does have a toothed projection on the base of the male flagellum, although, as indicated above, cannot be eliminated from *Neotrichodectes* s. str. on that basis. The form of the parameral plate of *N. wolffhuegeli* is much the same as members of *Neotrichodectes* s. str. and on this evidence the species is placed in the subgenus. Emerson (pers. comm.), however, suggests that the male genitalia of *N. wolffhuegeli* lie within the limits of permissible variation of *N. chilensis*, which he therefore considers as a junior synonym; *N. wolffhuegeli* and *N. chilensis* are found on the same host, although *N. chilensis* is also found on several other species of the host genus. All specimens identified as *N. wolffhuegeli* (by Werneck and in the present study) have a much narrower parameral plate than those identified as *N. chilensis*. However, the parameral plate, whilst not extending anteriorly between the b.a.l.s. in most specimens of *N. chilensis*, does do so in some. In those specimens of *N. chilensis* where there is no anterior extension of the parameral plate the endophallus lacks large, heavily-sclerotised teeth, or such teeth are few in number; in those where the extension is present the teeth are correspondingly more developed. The degree of development of the endophallus teeth seems to be proportional to the degree of development of the anterior margin of the parameral plate in *N. chilensis* and such teeth are present and well developed in *N. wolffhuegeli*. The sample of specimens of both species was too small to permit any correlations of genitalia type with host species or geographical distribution, though within *N. chilensis* specimens exhibiting both extremes were found from the same host in the same area. For the purposes of this study, the two species are treated as separate, *N. wolffhuegeli* is assigned to *Neotrichodectes* s. str., and *N. chilensis* is assigned to *Neotrichodectes (Conepaticola)*. This conclusion is regarded as the most satisfactory for the data presently available, but further collecting from species of the host genus (*Conepatus*) is needed to clarify the situation.

The original spelling of the species name *wolffhügeli* is emended here to *wolffhuegeli* in accordance with Article 32 (d)(i) of the *International Code of Zoological Nomenclature* (1984).

SPECIES INCLUDED

- mephitidis* (Packard, 1873) (c.50 ♂, c.100 ♀)
- minutus* (Paine, 1912) (64 ♂, 76 ♀)
- osborni* Kéler, 1944 (16 ♂, 21 ♀)
- thoracicus* (Osborn, 1902) (11 ♂, 9 ♀)
- wolffhuegeli* (Werneck, 1936) (1 ♂)

Subgenus **TRIGONODECTES** Kéler *gen. rev., stat. n.*

(Figs 227, 230, 235, 240)

Trigonodectes Kéler, 1944: 179, 185. Type-species: *Trichodectes barbarae* Neumann, by original designation.

DESCRIPTION. Anterior of head with osculum very shallow; clypeal marginal carina broadened medially into dorsal U-shaped sclerite with median posterior process; anterolateral margin of head convex; preantennal portion of head with outline rounded. Male flagellum with two basally-articulated 'teeth' distally, and with toothed projection present basally. Temple with long seta present on posterior margin.

Thoracic and abdominal setae long, abundant. Abdominal pleura lacking projections. Abdomen lacking sternal, tergal and pleural sclerites, except for lateral rods of male subgenital plate.

Gonapophyses slender, apically acute, sclerotised, with strong setae present along ventral margin; ventral lobe absent. Gonapophyses meet ventral vulval margin acutely. Ventral vulval margin with median lobulate projection, with margin not serrate, and submarginal setal row present (Fig. 235). Female genital chamber lacking lateral slanting scales and anterior sclerotised area on dorsal wall, but both ventral and dorsal walls bearing numerous scales with posterior spinules.

Parameral plate triangular or shield-shaped, pointed apically. Mesomer arch with median extension rounded, covered in small tubercles; mesomeres extend basally anterior to ends of b.a.l.s., and do not contact b.a.l.s. or parameral plate. Basal apodeme lacking postero-lateral projections on b.a.l.s. Male genitalia depicted in Fig. 240.

HOSTS. Mustelinae (Carnivora: Mustelidae).

COMMENTS. *Trigonodectes* has been treated as a synonym and a subgenus of *Trichodectes* (by Werneck, 1948 and Hopkins, 1949 respectively); in this study it is raised from synonymy with *Trichodectes* and *barbarae* is placed for the first time in *Neotrichodectes*. A more complete history of the varying status accorded to *Trigonodectes* is presented in Table 4.

SPECIES INCLUDED

barbarae (Neumann, 1913) *comb. n.* from *Trichodectes* (13 ♂, 13 ♀)

Subgenus **NASUICOLA** *subgen. n.*

(Figs 237, 239)

Type-species: *Trichodectes pallidus* Piaget.

DESCRIPTION. Anterior of head with osculum shallow; clypeal marginal carina broadened into dorsal rectangular sclerite; antero-lateral margin of head convex; preantennal portion of head not as long as postantennal portion, outline broadly rounded. Male flagellum with two basally-articulated 'teeth' distally, and with toothed projection present basally. Temple with long seta present on posterior margin.

Thoracic and abdominal setae long, abundant. Abdominal pleura lacking projections. Abdomen lacking sternal, tergal and pleural sclerites, except for lateral rods of male subgenital plate.

Gonapophyses with rounded ventral lobe with submarginal setae; spur distal to lobe very short. Gonapophyses meet ventral vulval margin acutely. Ventral vulval margin convex, but subgenital lobe or lobulate process not present. Female terminalia depicted in Fig. 237. Female genital chamber with dorsal wall bearing slanting scales laterally, spines medially (spines most apparent anteriorly, though may be obscured).

Parameral plate apically bifid, lacking median basal extension reaching anteriorly between b.a.l.s. Mesomer arch with median extension pointed; mesomeres basally abut postero-lateral extensions of b.a.l.s. Male genitalia depicted in Fig. 239.

HOSTS. Procyonidae (Carnivora).

SPECIES INCLUDED

pallidus (Piaget, 1880) [treated by previous authors as *Neotrichodectes* s. str.] (65 ♂, 75 ♀)

Subgenus **LAKSHMINARAYANELLA** Eichler *stat. n.*

(Figs 236, 241)

Lymeon Eichler, 1940: 158. Type-species: *Trichodectes gastrodes* Cummings, by monotypy. [Homonym of *Lymeon* Foerster, 1868: 176.]

Lakshminarayanelle Eichler, 1982: 83. [Replacement name for *Lymeon* Eichler.]

DESCRIPTION. Anterior of head with osculum present, deep; clypeal marginal carina broadened medially into posteriorly convex bar, parallel to curvature of osculum; antero-lateral margin of head straight or slightly sinuate; preantennal portion of head short in male, longer in female; outline broadly triangular. Male flagellum with seven basally-articulated 'teeth' distally, and with roughened projection present basally. Temple with no long setae present on posterior margin.

Thorax with dorsal setae of moderate length, longest on postero-lateral angle of pterothorax; pterothorax with setae sparse along posterior dorsal margin.

Abdominal setae of moderate length, not as long as segment except on posterior pleura; terga with lateral and median setal groups not clearly distinct, median gap sometimes pronounced. Abdominal pleura lacking projections. Abdomen lacking tergal and sternal sclerites except for lateral rods of male subgenital plate and tergite IX of female; abdominal pleura II, III, IV and, in female, VIII, with sclerites, though that of IV sometimes very small.

Gonapophyses broad, very thick; ventral lobe present, thick, with setae along posterior margin; spur distal to lobe not short, rounded apically (Fig. 236). Gonapophyses meet ventral vulval margin acutely. Ventral vulval margin convex, but subgenital lobe or lobulate process not present. Female genital chamber with dorsal wall bearing slanting scales laterally, spines medially (spines most apparent anteriorly).

Parameral plate apically bifid, sometimes projecting slightly anteriorly between b.a.l.s. Mesomeral arch with median extension pointed, broad basally; mesomeres basally abut postero-lateral extensions of b.a.l.s. Male genitalia depicted in Fig. 241.

HOSTS. Bradypodidae (Edentata).

SPECIES INCLUDED

cummingsi (Eichler, 1943) **comb. n.** from *Lakshminarayanella*

gastrodes (Cummings, 1916) **comb. n.** from *Lakshminarayanella* (4 ♂, 6 ♀, 4 nymphs)

Subgenus *CONEPATICOLA* **subgen. n.**

(Figs 231, 233, 234, 242)

Type-species: *Neotrichodectes semistriatus* Emerson & Price.

DESCRIPTION. Anterior of head with clypeal marginal carina broadened medially into dorsal U-shaped sclerite with median posterior process; antero-lateral margin of head convex or sinuate; preantennal portion of head not as long as postantennal portion, outline broadly rounded. Male flagellum with two basally-articulated 'teeth' distally, and with toothed projection basally. Temple with long seta present on posterior margin.

Thoracic and abdominal setae long, abundant. Abdominal pleura lacking projections. Abdomen lacking sternal and tergal sclerites, except for sternal rods of male subgenital plate and tergite IX of female; abdominal pleura II, III and VIII in female sometimes with sclerites, though that of III may be very small.

Gonapophyses with ventral lobe present, large, apparently comprising fused setal tubercles, with setae along posterior margin and anterior margin, the latter frequently directed posteriad; spur distal to lobe present, not short, frequently obtuse apically. Gonapophyses meet ventral vulval margin acutely. Ventral vulval margin convex, but subgenital lobe or lobulate process not present. Female terminalia depicted in Figs 233, 234. Female genital chamber with dorsal wall bearing slanting scales laterally, spines medially, sometimes lightly sclerotised and lacking scales, spines or other decoration antero-medially.

Parameral plate apically bifid, sometimes projecting slightly anteriorly between b.a.l.s. Mesomeral arch with median extension pointed; mesomeres basally abut postero-lateral extension of b.a.l.s. Male genitalia depicted in Fig. 242.

HOSTS. Mustelinae and Mephitinae (Carnivora: Mustelidae).

SPECIES INCLUDED

arizonae Werneck, 1948 (18 ♂, 39 ♀)

chilensis Werneck, 1948 (c. 50 ♂, c. 50 ♀)

interruptofasciatus (Kellogg & Ferris, 1915) (27 ♂, 46 ♀)

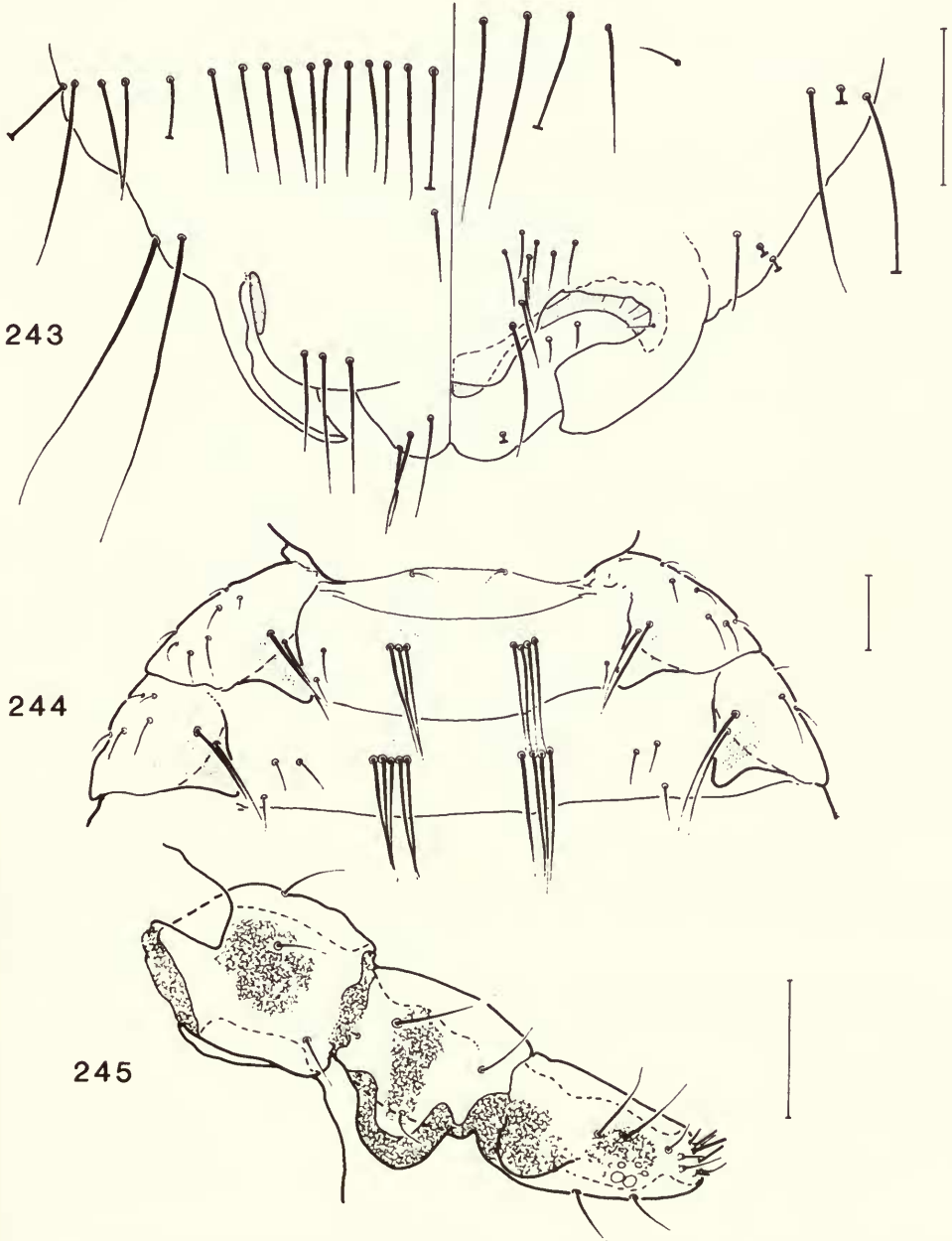
semistriatus Emerson & Price, 1976 (5 ♂, 5 ♀)

All the above species have been treated previously as *Neotrichodectes* s. str.

Genus *GEOMYDOECUS* Ewing

The genus *Geomydoecus* comprises two subgenera.

DESCRIPTION. Anterior of head with osculum present; dorsal preantennal sulcus present; clypeal marginal carina broadened medially into posteriorly convex bar; antero-lateral margin of head convex or sinuate; preantennal portion of head not long, outline broadly triangular or rounded. Temple margin broadly convex. Male scape expanded; longitudinal setal row present and comprising at least three setae; male scape sometimes with median posterior projection; flagellomeres fused in males and females; male flagellum with two basally-articulated 'teeth'; female pedicel with membranous postero-ventral projection (Fig. 245), sometimes obscure. Dorsum of head with setae short or of moderate length, more or less sparse; temple margin sometimes with specialised long, fine or short and stout latero-posterior setae*. Sitophore sclerite unmodified.



Figs 243–245 *Geomydoecus* species. 243, *G. (G.) californicus*, ♀ terminalia. 244, *G. (Thomomydoecus) asymmetricus*, ♂ anterior of abdomen, dorsal. 245, *G. (T.) pattoni*, ♀ antenna.

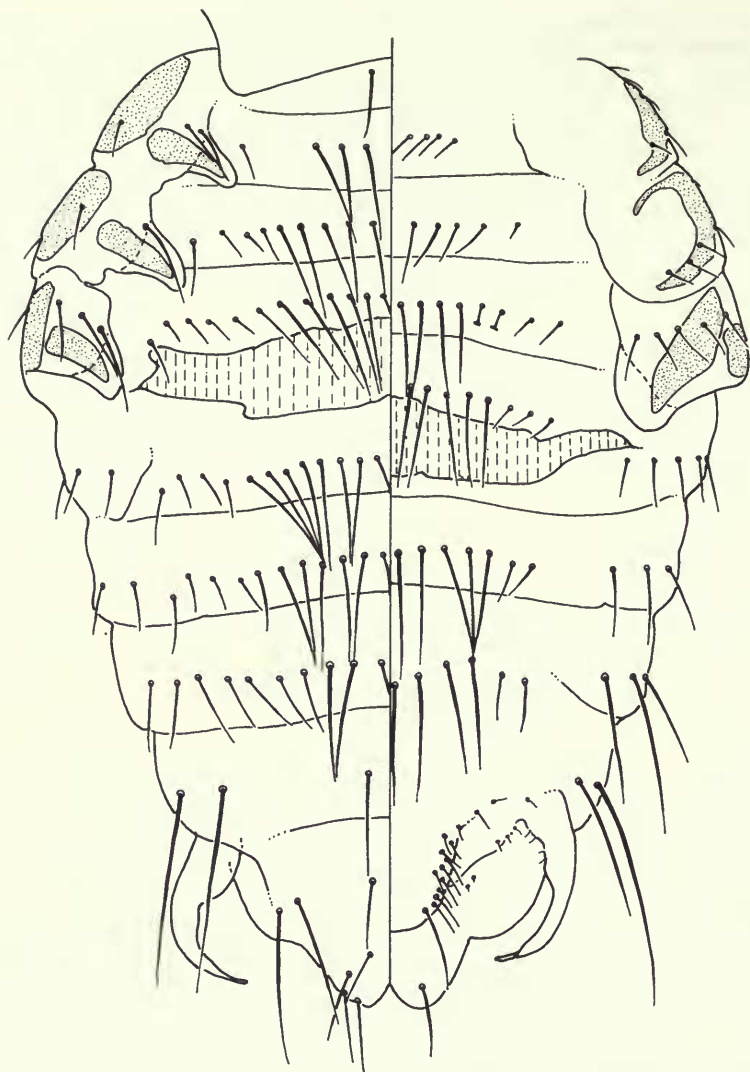
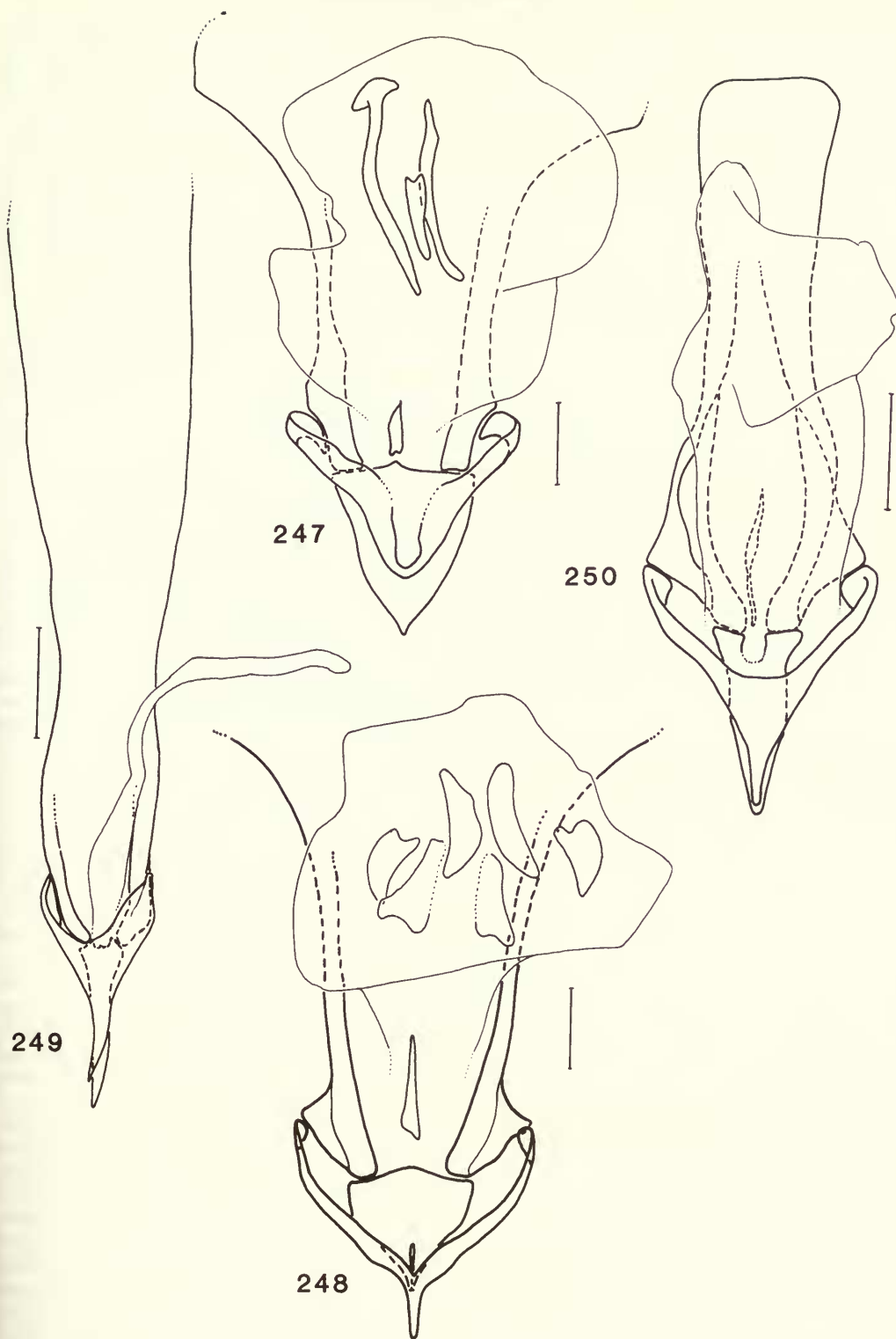


Fig. 246 *Georxydoecus* (*Thomomydoecus*) *minor*, ♀ abdomen. Hatched areas indicate damage to specimen.

Thorax with dorsal setae long or of moderate length; posterior margin of pronotum with four setae and wide median gap, posterior margin of pterothorax dorsally with varying number of marginal or submarginal setae.

Abdomen broadly rounded or more elongate and tapered, particularly in male. Abdominal spiracles absent. Abdomen with at least some setae as long as segment; setae generally abundant; terga, especially of males, with median and lateral setal groups distinct, though median groups generally united; male terga II–VI without median setae shorter than others; male terga II and III sometimes with median group comprising exceptionally long, stout setae* (Fig. 244); anterior setae present on pleura II and III only; postero-lateral setae sometimes clearly present (Fig. 244), otherwise obscured, though may be present as most lateral seta of lateral group, which is frequently situated more posteriorly than other setae. Abdominal pleura with projections dorsally on pleura II, III, IV and, at least in female, ventrally on IV, sclerotised (Fig. 246) or unsclerotised*; projections generally more apparent in females than males. Abdominal terga and sterna lacking sclerites, except for lateral rods of male subgenital plate and, sometimes, terga II–IV of male*; abdominal pleura II and sometimes III and IV sclerotised, at least in female; other pleura unsclerotised.



Figs 247–250 *Geomydoecus* species, ♂ genitalia. 247, *G. (G.) thomomyus*. 248, *G. (G.) actusosi*. 249, *G. (Thomomydoecus) minor*. 250, *G. (T.) wardi*.

Gonapophyses broad, membranous, with ventral marginal setae, if present, generally basal only; ventral lobe absent (Figs 243, 246). Gonapophyses meet ventral vulval margin smoothly or acutely, but not linked by sclerotised band. Ventral vulval margin not sclerotised; generally convex or very convex medially; subgenital lobe not present. Female genital chamber with dorsal wall bearing slanting scales laterally, lightly sclerotised and lacking scales or other decoration antero-medially. Common oviduct generally with distinct striae.

Male subgenital plate with only s.g.p.r. present. Pseudostyli absent. Male genital opening dorsal. Parameres fused to form single plate with apex pointed or bifid*. Basiparameral sclerites absent. Mesomeres fused apically; mesomeral arch with or without median extension; mesomeres basally about b.a.l.s., which sometimes have postero-lateral extensions; mesomeres do not contact parameral plate. Male genitalia depicted in Figs 247–250.

HOSTS. Geomyidae (Rodentia).

COMMENTS. A few of the species are parthenogenetic.

No more than 25 specimens of most species were examined during the course of this study, though in many cases large numbers were available.

Detailed descriptions of all species of *Geomydoecus* s.l. and a phenetic treatment of the genus may be found in Hellenthal & Price (1976, 1980), Price (1974, 1975), Price & Emerson (1971, 1972), Price & Hellenthal (1975a, 1975b, 1976, 1979, 1980a, 1980b, 1980c, 1981a, 1981b), Price & Timm (1979), Timm & Price (1979, 1980).

Subgenus *GEOMYDOECUS* Ewing

(Figs 243, 247, 248)

Geomydoecus Ewing, 1929: 193. Type-species: *Trichodectes geomydis* Osborn, by original designation.

DESCRIPTION. Temple margin sometimes with two short, stout setae latero-posteriorly, or single long, fine seta latero-posteriorly.

Male abdominal terga II and III only rarely with median setal group comprising exceptionally long, stout setae (*G. copei*). Pleural projections rarely sclerotised. Male terga II–IV not sclerotised.

Male genitalia not asymmetric. Parameral plate apically pointed or bifid. Male genitalia depicted in Figs 247, 248.

HOSTS. Geomyidae (Rodentia).

SPECIES INCLUDED

- actuosi* Price & Hellenthal, 1981 (25 ♂, 25 ♀)
- albat*i Price & Hellenthal, 1981 (25 ♂, 25 ♀)
- alcorni* Price & Emerson, 1971 (6 ♂, 6 ♀)
- alleni* Price & Emerson, 1971 (2 ♂, 6 ♀)
- angularis* Price & Hellenthal, 1981 (25 ♂, 25 ♀)
- aurei aurei* Price & Hellenthal, 1981 (25 ♂, 25 ♀)
- aurei grahamensis* Price & Hellenthal, 1981 (25 ♂, 25 ♀)
- bajaiensis* Price & Hellenthal, 1981 (25 ♂, 25 ♀)
- bulleri* Price & Emerson, 1971 (25 ♂, 25 ♀)
- californicus* (Chapman, 1897) (25 ♂, 25 ♀)
- centralis* Price & Hellenthal, 1981 (25 ♂, 25 ♀)
- chapini* Werneck, 1945 (12 ♂, 16 ♀)
- cherriei* Price, 1974
- chiapensis* Price & Emerson, 1971 (18 ♂, 20 ♀)
- chihuahuae chihuahuae* Price & Hellenthal, 1979 (25 ♂, 25 ♀)
- chihuahuae emersoni* Price & Hellenthal, 1979 (25 ♂, 17 ♀)
- clausonae* Price & Hellenthal, 1981 (25 ♂, 25 ♀)
- cliftoni* Price & Hellenthal, 1981 (25 ♂, 25 ♀)
- copei* Werneck, 1945 (25 ♂, 25 ♀)
- coronadoi* Barrera, 1961 (25 ♂, 25 ♀)
- costaricensis* Price & Emerson, 1971 (7 ♂, 7 ♀)
- crovelloi* Price & Hellenthal, 1981 (25 ♂, 25 ♀)
- dakotensis* Price & Emerson, 1971 (25 ♂, 25 ♀)
- dagleishi* Timm & Price, 1979 (2 ♂, 2 ♀)

- dariensis* Price & Emerson, 1971 (10 ♂, 14 ♀)
duchesnensis Price & Emerson, 1971 (5 ♂, 8 ♀)
ewingi Price & Emerson, 1971 (25 ♂, 25 ♀)
expansus (Duges, 1902) (25 ♂, 25 ♀)
extimi Price & Hellenthal, 1981 (26 ♂, 25 ♀)
fulvescens Price & Emerson, 1971 (25 ♂, 25 ♀)
fulvi Price & Hellenthal, 1979 (25 ♂, 25 ♀)
geomydis (Osborn, 1891) (25 ♂, 25 ♀)
guadalupensis Hellenthal & Price, 1980 (25 ♂, 25 ♀)
heaneyi Timm & Price, 1980 (25 ♂, 25 ♀)
hoffmanni Price & Hellenthal, 1976 (25 ♂, 25 ♀)
hueyi Price & Hellenthal, 1980 (25 ♂, 25 ♀)
idahoensis Price & Emerson, 1971 (25 ♂, 25 ♀)
illinoensis Price & Emerson, 1971 (25 ♂, 25 ♀)
jaliscoensis Price & Hellenthal, 1981 (25 ♂, 25 ♀)
jonesi Price & Emerson, 1971 (4 ♂, 5 ♀)
limitaris limitaris Price & Hellenthal, 1981 (25 ♂, 25 ♀)
limitaris bakeri Price & Hellenthal, 1981 (25 ♂, 25 ♀)
limitaris halli Price & Hellenthal, 1981 (25 ♂, 25 ♀)
limitaris tolteci Price & Hellenthal, 1981 (25 ♂, 25 ♀)
martini Price & Hellenthal, 1975 (25 ♂, 25 ♀)
mcgregori Price & Emerson, 1971 (25 ♂, 25 ♀)
merriami Price & Emerson, 1971 (25 ♂, 25 ♀)
mexicanus Price & Emerson, 1971 (25 ♂, 25 ♀)
mobilensis Price, 1975 (25 ♀)
musculi Price & Hellenthal, 1981 (25 ♂, 25 ♀)
nayaritensis Price & Hellenthal, 1981 (16 ♂, 25 ♀)
nebrathkensis Timm & Price, 1980 (25 ♂, 25 ♀)
oklahomensis Price & Emerson, 1971 (25 ♂, 25 ♀)
oregonus Price & Emerson, 1971 (25 ♂, 25 ♀)
panamensis Price & Emerson, 1971 (23 ♂, 22 ♀)
pattoni Price & Hellenthal, 1979 (12 ♂, 8 ♀)
perotensis perotensis Price & Emerson, 1971 (25 ♂, 25 ♀)
perotensis irolonis Price & Emerson, 1971 (25 ♂, 25 ♀)
polydentatus Price & Emerson, 1971 (25 ♂, 25 ♀)
quadridentatus Price & Emerson, 1971 (25 ♂, 25 ♀)
scleritus (McGregor, 1917) (3 ♂, 25 ♀)
setzeri Price, 1974 (6 ♂, 8 ♀)
shastensis Price & Hellenthal, 1980 (25 ♂, 25 ♀)
sinaloae Price & Hellenthal, 1981 (25 ♂, 25 ♀)
spickai Timm & Price, 1980 (25 ♂, 25 ♀)
subcalifornicus Price & Emerson, 1971 (25 ♂, 25 ♀)
subgeomydis Price & Emerson, 1971 (25 ♂, 25 ♀)
subnubili Price & Hellenthal, 1975 (25 ♂, 25 ♀)
tamaulipensis Price & Hellenthal, 1975 (3 ♂, 25 ♀)
texanus texanus Ewing, 1936 (25 ♂, 25 ♀)
texanus tropicalis Price & Hellenthal, 1975 (25 ♂, 25 ♀)
thomomyus (McGregor, 1917) (25 ♂, 25 ♀)
tolucae Price & Emerson, 1971 (25 ♂, 25 ♀)
traubi Price & Emerson, 1971 (25 ♂, 25 ♀)
trichopi Price & Emerson, 1971 (25 ♂, 25 ♀)
truncatus Werneck, 1950 (25 ♂, 25 ♀)
umbrini Price & Emerson, 1971 (25 ♂, 25 ♀)
ustulati ustulati Price & Hellenthal, 1975 (25 ♂, 25 ♀)
ustulati clarkii Price & Hellenthal, 1975 (25 ♂, 25 ♀)
veracruzensis Price & Emerson, 1971 (25 ♂, 25 ♀)
warmanae Price & Hellenthal, 1981 (25 ♂, 25 ♀)
welleri welleri Price & Hellenthal, 1981 (25 ♂, 25 ♀)
welleri multilineatus Price & Hellenthal, 1981 (25 ♂, 25 ♀)

wernecki Price & Emerson, 1971 (25 ♂, 25 ♀)
yucatanensis Price & Emerson, 1971 (25 ♂, 25 ♀)

Subgenus *THOMOMYDOECUS* Price & Emerson

(Figs 244–246, 249, 250)

Thomomydoecus Price & Emerson, 1972: 464 [as subgenus of *Geomydoecus* Ewing]. Type-species: *Geomydoecus (Thomomydoecus) jamesbeeri* Price & Emerson, by original designation.

DESCRIPTION. Temple margin with single stout seta and finer, shorter adjacent setae latero-posteriorly.

Male abdominal terga II and III with median setal group comprising exceptionally long, stout setae. Pleural projections sclerotised, at least in female (Fig. 246). Male terga II–IV sometimes with sclerites.

Gonapophyses meet vulval margin smoothly.

Male genitalia symmetric (Fig. 250) or asymmetric (Fig. 249). Parameral plate apically pointed.

HOSTS. *Thomomys* spp. (Rodentia: Geomyidae).

COMMENTS. As discussed on p. 232, the subgenus *Geomydoecus* is probably paraphyletic and *Thomomydoecus* paraphyletic or even polyphyletic. *Geomydoecus (Thomomydoecus)* was raised to generic status by Hellenthal & Price (1984), on the basis that there are 'sufficient' morphological differences between it and *Geomydoecus* s. str. This action, reversed here, is consistent with the purely phenetic approach employed by the authors, but cannot be reconciled with the cladistic methods used in this study. The division of *Geomydoecus* into subgenera is retained, even though neither of the two subgenera is 'natural' (i.e. holophyletic), because insufficient work has been done to resolve the relationships properly, and the independent unit of the classification, the genus *Geomydoecus*, is holophyletic. Raising *Thomomydoecus* to generic status, however, would produce two independent units in the classification (*Geomydoecus* and *Thomomydoecus*) that differ from all the others in not being holophyletic.

Geomydoecus (T.) byersi (Hellenthal & Price) was described after the completion of this manuscript and has not been included in the cladistic analysis.

SPECIES INCLUDED

asymmetricus Price & Hellenthal, 1980 (25 ♂, 25 ♀)
birneyi Price & Hellenthal, 1980 (25 ♂, 25 ♀)
byersi (Hellenthal & Price, 1984) **comb. n.** from *Thomomydoecus*
dickermani Price & Emerson, 1972 (25 ♂, 25 ♀)
genowaysi Price & Emerson, 1972 (25 ♂, 25 ♀)
greeri Price & Hellenthal, 1980 (2 ♂)
jamesbeeri Price & Emerson, 1972 (8 ♂, 10 ♀)
johnhafneri Price & Hellenthal, 1980 (25 ♂, 25 ♀)
markhafneri Price & Hellenthal, 1980 (25 ♂, 25 ♀)
minor Werneck, 1950 (25 ♂, 25 ♀)
neocopei Price & Emerson, 1971 (2 ♂, 1 ♀)
orizabae Price & Hellenthal, 1980 (10 ♂, 26 ♀)
peregrini Price & Hellenthal, 1980 (4 ♂, 4 ♀)
potteri Price & Hellenthal, 1980 (16 ♂, 25 ♀)
timmi Price & Hellenthal, 1980 (25 ♂, 25 ♀)
wardi Price & Emerson, 1971 (25 ♂, 25 ♀)
williamsi Price & Hellenthal, 1980 (8 ♂, 16 ♀)
zacatecae Price & Hellenthal, 1980 (25 ♂, 25 ♀)

Keys to Trichodectidae

Two keys are provided: a key to subfamilies and a key to genera and subgenera. The latter key contains all genera and subgenera, and it is not necessary to use the subfamily key as an introduction to it.

The subfamily key is included because of the formal requirement that any newly described taxon must be accompanied by some form of description in order to make the name available. The key to the five subfamilies of Trichodectidae therefore serves to distinguish Neotrichodectinae subfam. n. from all others.

Key to subfamilies

- 1 No abdominal spiracles present; majority of tergal and sternal setae at least two-thirds length of segment or, if not, median setal group on tergum II comprising at least three setae (and, frequently, median groups running together). New World
NEOTRICHODECTINAE subfam. n. (p. 321)
- At least one pair of abdominal spiracles present or, if not, majority of abdominal sternal and tergal setae less than two-thirds length of segment or median setal group on tergum II comprising only one seta. Old and New World 2
- 2 Female subgenital lobe present, frequently with serrate margin, at least posteriorly; if margin of subgenital lobe smooth, gonapophyses meet vulval margin smoothly (Fig. 153); female flagellomeres fused; abdominal spiracles numbering six or fewer pairs. Parasitic on Carnivora and Primates. Old and New World **TRICHODECTINAE** Kellogg, 1896 (p. 286)
- Female subgenital lobe absent or, if present, not marginally serrate and gonapophyses meet vulval margin acutely; female flagellomeres fused or unfused; abdominal spiracles numbering six pairs, though spiracles on segment VIII may be very small and inconspicuous, possibly non-functional (some species of *Procaviphilus* (*Meganarionoides*)). Not parasitic on Carnivora. Old and New World 3
- 3 Dorsal or ventral projection present on abdominal pleurum IV; mesomer al arch generally produced basally between b.a.l.s.; female antennal flagellomeres generally not fused, or only partially fused; parasitic on hyraxes and primates. Old and New World
DASYONYGINAE Kéler, 1938 (p. 267)
- Pleurum IV lacking any projection; mesomer al arch rarely produced basally between b.a.l.s.; female flagellomeres generally fused or, if not, then female with long setal tufts on abdominal pleura VIII and IX; not parasitic on hyraxes or primates 4
- 4 Posterior margin of temple generally produced, very convex; (Fig. 87); very long setae present on at least pleurum VIII, sometimes also on pleura VII (male) or IX (female); basiparameral sclerites present; mesomer al arch lacking extension if complete, otherwise tripartite, median part sometimes obscure (Figs 91, 93); if mesomer al arch entire, male genitalia as in Fig. 89, temple margins not greatly produced, and female with two flagellomeres; parasitic on New World porcupines (Erethizontidae) **EUTRICHOPHILINAE** Kéler, 1938 (p. 265)
- Temples not so developed; setae on pleurum VIII not exceptionally long; basiparameral sclerite present or absent; mesomer al arch, if present, with or without extension, but arch never tripartite; female flagellomeres fused; pseudostyli frequently present; parasitic on Artiodactyla and Perissodactyla. Old and New World **BOVICOLINAE** Kéler, 1938 (p. 247)

Key to genera and subgenera

- 1 No abdominal spiracles present; majority of tergal and sternal setae at least two-thirds length of segment or, if not, median setal group on tergum II comprising at least three setae (and, frequently, median groups running together). New World 2
- At least one pair of abdominal spiracles present or, if not, majority of abdominal sternal and tergal setae less than two-thirds length of segment or median setal group on tergum II comprising only one seta. Old and New World 8
- 2 Abdominal pleura II-IV with dorsal projections (Fig. 246), though most apparent in females and sometimes very inconspicuous; male lacking tergo central microsetae; latero-posterior corner of temple margin frequently with single long fine seta or one or two shorter, stout setae; female pedicel with dorsal membranous projection (Fig. 245) (sometimes obscure). [Geomyidae] (**GEOMYDOECUS** s.l., p. 328) 3
- Abdominal pleura lacking dorsal projections, or single membranous projection present on pleurum IV only (Fig. 228); male with tergo central microsetae on abdominal terga II-VI (Fig. 227); long seta frequently present on temple margin but shorter stout seta not developed; female pedicel lacking any projection. (**NEOTRICHODECTES** s.l., p. 321) 4
- 3 Pleural projections on pleurum II sclerotised; temple margin with single stout seta and associated smaller finer setae; male abdominal terga II and III with rows of enlarged setae (Fig. 244); parameral plate with single apical point; male genitalia symmetric or asymmetric
GEOMYDOECUS (THOMOMYDOECUS) (p. 334)
- Pleural projection on pleurum II unsclerotised or, if sclerotised, posterolateral temple margin

- with single long fine seta and associated smaller setae; temple margin with or without specialised setae but not with single stout seta; male abdominal terga II and III rarely with rows of specialised setae (*G. copei* only); parameral plate with single apical point or apically bifid; male genitalia symmetric **GEOMYDOECUS (GEOMYDOECUS)**(p. 332)
- 4 Female subgenital lobe present, with serrate margins; female genital chamber with clear, flat dorsal region but lacking single scattered spines; gonapophyses broad, membranous, lacking lobe; parameral plate slender, with basal projection between b.a.l.s. (Fig. 238). [Mustelidae and Procyonidae] **NEOTRICHODECTES (NEOTRICHODECTES)**(p. 326)
- Female subgenital lobe absent or, if present, lobe with smooth margins and longitudinal setal rows (Fig. 235); female genital chamber, if with clear flat dorsal area, then with single spines scattered over it; gonapophyses not broad and membranous, frequently with lobe; parameral plate broad, with very limited projection between b.a.l.s. 5
- 5 Ventral vulval margin with lobulate process with smooth margins and longitudinal rows of setae (Fig. 235); gonapophyses slender, sclerotised, lacking lobe; parameral plate with single apical point; mesomeral arch extension broad, clubbed (Fig. 240). [Mustelidae] **NEOTRICHODECTES (TRIGONODECTES)**(p. 327)
- Ventral vulval margin convex, but not produced; gonapophyses not slender, lobe present; parameral plate with apex bifid; mesomeral arch with pointed extension 6
- 6 Large species, over 2.75 mm long; male flagellum with 7 articulated 'teeth'; female gonapophyses thick, with lobe and spur (Fig. 236); female pleurum VIII sclerotised; abdominal setae relatively small, not attaining following setal row. [Bradypodidae] **NEOTRICHODECTES (LAKSHMINARAYANELLA)**(p. 327)
- Smaller species, under 2.25 mm long; male flagellum with 2 articulated 'teeth'; female gonapophyses otherwise; female pleurum VIII not sclerotised; abdominal setae long, attaining or nearly attaining setal bases of following setal row. [Carnivora] 7
- 7 Gonapophyses with flat lobe and small spur (Fig. 237); male mesomeral arch extension attaining end of parameral plate (Fig. 239) [Procyonidae] **NEOTRICHODECTES (NASUICOLA)**(p. 327)
- Gonapophyses with lobe comprising fused setal tubercles, long spur present (Fig. 233); male mesomeral arch extension reaching beyond apex of parameral plate (Fig. 242). [Mustelidae] **NEOTRICHODECTES (CONEPATICOLA)**(p. 328)
- 8 Five pairs of abdominal spiracles present; vulval margin sclerotised, with or without setal tubercles, and meeting gonapophyses smoothly; subgenital lobe present; parameres not fused to b.a.l.s.; mesomeres absent; postcoxale absent; abdominal segments II–V with median setal group present, comprising at least three setae. [Mustelidae] **TRICHODECTES (PARATRICHODECTES)**(p. 300)
- Other than five pairs of abdominal spiracles present, though spiracles on segment VIII may be very small, inconspicuous and possibly non-functional (some species of *Procaviphilus* (*Meganarionoides*) as described in key couplet 26, and some species of *Trichodectes* (*Stachiella*), as described in key couplet 14) 9
- 9 Abdominal pleura V–VI (at least) lacking setae 10
- Abdominal pleura III–VIII (at least) with posterior setal row and, sometimes, anterior setae ... 12
- 10 Abdominal tergal setae on segments I–VI less than half length of segment, shorter than postero-lateral setae; pleura V–VI lacking setae (Fig. 159); male flagellum with two basally-articulated 'teeth'; mesomeres present, unfused; parameres fused, with distinct inturned apices arising from plate (Fig. 171); subgenital lobe bifurcate, with long basal lateral processes (Fig. 149). [Mustelidae] **TRICHODECTES (TRICHODECTES)** (in part) (p. 299)
- At least some setae on abdominal terga I–III as long or longer than segment and postero-lateral seta, and postero-lateral setae sometimes absent; pleura IV–VII (at least) lacking setae (Fig. 141); male flagellum lacking 'teeth'; mesomeres absent; parameres unfused or united at base only; subgenital lobe not bifurcate or only slightly so; basal processes of subgenital lobe absent or, if present, not long (Fig. 146). [Lutrinae] 11
- 11 Posterior setal row present on pleurum III; parameres slender, rod-like, fused basally (Figs 144, 145); subgenital lobe lacking basal lateral processes; gonapophyses lacking setal tubercles (Fig. 143) **LUTRIDIA** (p. 288)
- Posterior setal row not present on pleurum III; parameres broad, not fused to each other (Fig.

- 147); subgenital lobe with basal lateral processes; gonapophyses with setal tubercles (Fig. 146) **NEOLUTRIDIA** (p. 289)
- 12 Ventral vulval margin meets gonapophyses smoothly, joined by sclerotised band; subgenital lobe present, frequently with basal lateral processes; sternal setae on at least segments III–VI attaining or nearly attaining base of following setal row; dorsum of head with setae sparse; male scape expanded or, if not, parameres fused to b.a.l.s. 13
- Ventral vulval margin meets gonapophyses acutely or, if meeting smoothly, not joined by sclerotised band; subgenital lobe present or absent, but, if present, never with basal lateral processes (except *Damalinia* (*Tricholipeurus*) *elongata*; see Fig. 65); sternal setae on segments III–VI not attaining base of following setal row, usually less than three-quarters length of segment or, if longer, either female genitalia not as described and dorsum of head with dense setal covering (*Bovicola* (*Holakartikos*) and *B. (Spinibovicola)*) or male scape not expanded and parameres not fused to b.a.l.s. 15
- 13 Pleurum IV with dorsal projection; anterior setae present on abdominal terga and sterna. [Ursidae]..... **WERNECKODECTES** (p. 290)
- Pleurum IV without dorsal projection; anterior setae not present on abdominal terga and sterna 14
- 14 Male abdominal terga II–IV (at least) with median setal group reduced to one seta (Fig. 164); parameres fused to b.a.l.s. (Figs 172, 174) or characteristically asymmetric (Fig. 173); female abdominal terga III–VII (at least) with median setal group reduced to one seta or absent. [Mustelidae and Procyonidae] **TRICHODECTES (STACHIELLA)** (p. 301)
- Tergal setae of both sexes more abundant, with at least two setae in median setal group; parameres not fused to b.a.l.s. [Canidae, Viverridae, Ursidae and Mustelidae] **TRICHODECTES (TRICHODECTES)** (in part) (p. 299)
- 15 Posterior setal row of pleurum III with setae stouter than those of p.s.r. of pleurum V (Figs 182, 188) or, if not, species with four pairs of abdominal spiracles; otherwise species with 0, 1, 2, 3, 4 or 6 pairs of abdominal spiracles; subgenital lobe present; gonapophyses with lobe present 16
- Posterior setal row of pleurum III with setae not stouter than those of p.s.r. of pleurum V; six pairs of abdominal spiracles present, if gonapophyses with lobe, then subgenital lobe absent 19
- 16 Abdominal spiracles numbering 6, 4 or 0 pairs; if no abdominal spiracles present, then female with gonopore surrounded by spicular refringent patch, or gonapophysis lobe comprising two fused tubercles, or antennal sensilla in pit with peripheral tongue-like projections; female subgenital lobe frequently with overlapping scales or spines; male mesomeral arch always present, with median extension or two apical nipples; mesomeres produced basally between b.a.l.s. or, if not, antennal sensilla as described above; parameres usually broad, contacting mesomeres only, not b.a.l.s.; male abdominal tergum II lacking specialised setae of median group. (**LORISICOLA** s.l., p. 312) 17
- Abdominal spiracles numbering 3, 2, 1 or 0 pairs; if no abdominal spiracles present, then female gonopore not surrounded by spicular refringent patch, gonapophysis lobe not comprising two fused setal tubercles; antennal sensilla of male and female never in pit with peripheral tongue-like projections; female subgenital lobe never with overlapping scales or spines; male mesomeres fused, unfused or absent; if mesomeres fused, mesomeral arch never with median extension or apical nipples; parameres frequently narrow, rod-like, contacting mesomeres, b.a.l.s. or both; male abdominal tergum II frequently with long, specialised setae (Figs 179, 180, 187–189). (**FELICOLA** s.l., p. 302) 18
- 17 Male antennal flagellum with ‘teeth’ on projection; six pairs of abdominal spiracles present or abdominal spiracles absent, in which case antennal sensilla in pit with peripheral tongue-like projections. [Felidae, Viverridae and Lorisidae]..... **LORISICOLA (LORISICOLA)** (p. 316)
- Male antennal flagellum with ‘teeth’ not on projection, or, if projection present, mesomeral arch lacking extension; four pairs of abdominal spiracles present or abdominal spiracles absent, in which case male gonopore surrounded by spicular patch (Fig. 225). [Viverridae and Herpestidae] **LORISICOLA (PARADOXUROECUS)** (p. 318)
- 18 Male antennal flagellum with one or three basally-articulated ‘teeth’, or ‘teeth’ absent, in which case male abdominal tergum III with median setal group reduced to one seta of similar size to those on tergum II, which are not greatly enlarged, and parameres not fused; female gonapophysis with lobe and spur present, lobe rounded or rectangular and formed of fused tubercles; subgenital lobe bifid or not; if subgenital lobe bifid, lobes pointed, rounded or with

rectangularly obtuse posterior margins (Fig. 176); everted portion of male endophallus never sclerotised; abdominal spiracles numbering 0, 1 or 3 pairs. [Herpestidae and Canidae]

FELICOLA (SURICATOECUS)(p. 312)

- Male antennal flagellum with one, two, three or four nonarticulated 'teeth', or 'teeth' absent, in which case male abdominal tergum III with median setal group reduced to one seta much smaller than those on tergum II, which are greatly enlarged, and parameres fused, at least basally; female with gonapophysis lobe rounded, with or without spur, but lobe never rectangular; subgenital lobe bifid or not; if subgenital lobe bifid, lobes of various shapes, but never with rectangularly obtuse posterior margins; everted portion of male endophallus frequently thinly sclerotised (Figs 190, 196); abdominal spiracles numbering 0, 2 or 3 pairs. [Herpestidae, Viverridae and Felidae] **FELICOLA (FELICOLA)**(p. 302)
- 19 Dorsal or ventral projection present on abdominal pleurum IV (Fig. 105); mesomer arch generally produced basally between b.a.l.s.; female antennal flagellomeres generally not fused, or only partially fused. [Procaviidae and Primates] 20
- Pleurum IV lacking any projection; mesomer arch rarely produced basally between b.a.l.s.; female flagellomeres generally fused or, if not, then female with long setal tufts on abdominal pleura VIII and IX (see couplet 27); not parasitic on hyraxes or primates 27
- 20 Sitophore sclerite modified, with posterior arms extended (Fig. 12) (sclerite difficult to see) 21
- Sitophore sclerite unmodified (Fig. 11) (not, generally, difficult to see) 23
- 21 Tarsal claws with ventral teeth or spines; temple margin with or without small rounded projection; pleural projection on abdominal pleurum IV not elongate. [Procaviidae] (**DASYONYX**s.l., p. 279) 22
- Tarsal claws lacking ventral teeth or spines; temple margin with long, broad, triangular projection (Fig. 138); pleural projection on abdominal pleurum IV long (Fig. 136). [Procaviidae] **EURYTRICHODECTES**(p. 284)
- 22 Tarsal claws with sharp, fine spines (Fig. 14) **DASYONYX (DASYONYX)**(p. 282)
- Tarsal claws with broad, saw-like teeth (Fig. 15) **DASYONYX (NEODASYONYX)**(p. 284)
- 23 Abdominal sternum II with broad, heavily-sclerotised band articulated with abdominal pleurum II (Fig. 105); setal row of male scape comprising only two setae; basiparameral sclerites present. [Procaviidae] (**PROCAVICOLA** s.l., p. 270) 24
- Abdominal sternum II lacking sclerotised band or, if sclerotised band present, this is fused to abdominal pleurum II or medially broken; setal row of male scape numbering more than two setae; basiparameral sclerites absent or, if present, thoracic spiracle with tubular atrium and female flagellomeres fused 25
- 24 Posterior angle of temple with small projection; mesomer arch with lateral double flexion and median extension; endophallus with large hook-like spines (Fig. 107) **PROCAVICOLA (CONDYLOCEPHALUS)**(p. 274)
- Posterior angle of temple lacking projection; mesomer unfused and lacking lateral double flexion and median extension; endophallus lacking large hook-like spines (Fig. 109) **PROCAVICOLA (PROCAVICOLA)**(p. 270)
- 25 Atrium of thoracic spiracle spherical; mesomer arch with median extension and lateral desclerotisations; gonapophyses with setal tubercles or, if not, postcoxale greatly developed and fused to abdominal pleurum II. [Procaviidae and Cercopithecidae] (**PROCAVIPHILUS** s.l., p. 274) 26
- Atrium of thoracic spiracle tubular; mesomer arch lacking median extension and not desclerotised laterally; gonapophyses lacking setal tubercles; postcoxale not greatly developed and fused to abdominal pleurum II. [Cebidae] **CEBIDICOLA**(p. 267)
- 26 Parameres with basal flange, sometimes fused faintly; perisetal gap of male subgenital plate absent; postcoxale not fused to abdominal pleurum II; setal tubercles of gonapophyses not fused characteristically. [Procaviidae] **PROCAVIPHILUS (PROCAVIPHILUS)**(p. 278)
- Parameres usually lacking basal flange; perisetal gap of male subgenital plate present or, if absent, parameres fused together and articulated with mesomer arch as in Fig. 120, and mesomer arch produced basally along b.a.l.s. (Fig. 121); postcoxale fused to abdominal pleurum II, at least in females; setal tubercles of gonapophyses fused characteristically (Fig. 111) or, if not, ventral vulval margin as in Fig. 113. [Procaviidae and Cercopithecidae] **PROCAVIPHILUS (MEGANARIONOIDES)**(p. 278)

- 27 Posterior margins of temple generally produced, very convex (Fig. 87); very long setae present on at least pleurum VIII (Figs 88, 90), sometimes also on pleurum VII (males) or IX (female); basiparameral sclerites present; mesomer arch lacking extension if complete, otherwise tripartite, median part sometimes obscure (Figs 101, 102); if mesomer arch entire, male genitalia as in Fig. 100, temples not greatly produced, and female with two flagellomeres, otherwise female flagellomeres fused. [Erethizontidae] **EUTRICHOPHILUS**(p. 265)
- Temples not so developed; setae on pleurum VIII not exceptionally long; basiparameral sclerites present or absent; mesomer arch, if present, with or without extension, but never tripartite; female flagellomeres fused 28
- 28 Parameres narrow, rod-like and fused basally; mesomer arch with broad lobe-like extension; b.a.l.s. widely divergent anteriorly (Fig. 139); gonapophyses with setal tubercles; pseudostyli absent. [Protelidae and Hyaenidae] **PROTELICOLA**(p. 286)
- Parameres not narrow and fused basally or, if so, then b.a.l.s. not widely divergent anteriorly; mesomer arch without broad lobulate extension; gonapophyses lacking setal tubercles; pseudostyli frequently present 29
- 29 Subgenital lobe present; endophallus with dense patch of regularly-arranged spicules or, if not, parameral plate with single apex (Fig. 81); mesomer arch entire, with abrupt bend to enable bases to meet parameres (Figs 81, 82), or mesomeres unfused and b.a.l.s. with anteposterior spur (Fig. 83); interior face of male flagellum serrate (Fig. 13); abdominal sterna never with anterior setae; long, slender species. [Bovidae and Cervidae] **DAMALINIA (TRICHOLOPEURUS)**(p. 264)
- Subgenital lobe absent or, if present, as small flap (Fig. 42) and species with anterior setae on abdominal sterna (*Bovicola jellisoni*); sternum VII sometimes developed posteriorly into two projecting spikes (*Damalinia theileri*, *neotheileri* and *semitheileri*, Fig. 73); endophallus lacking spicular patch; parameres with apices free; mesomeres apically fused, unfused or absent, but abrupt bend not present; b.a.l.s. lacking anteposterior spur; interior face of male flagellum without serrations; broader species 30
- 30 Dorsal face of vulva with pointed scales; gonapophyses hook-shaped (Fig. 66); common oviduct, at branching point, with folded and more or less apparent collar, sometimes partially sclerotised and refracting transmitted light; mesomeres unfused; abdominal pleurum never extending ventrally onto abdominal sternum II; interior face of male flagellum serrate. [Bovidae and Cervidae] **DAMALINIA (CERVICOLA)**(p. 263)
- Dorsal face of vulva lacking pointed scales; gonapophyses not hook-shaped or, if they are, then abdominal pleurum II extending onto sternum II (Fig. 68); common oviduct lacking 'collar' as described above; mesomeres fused, unfused or absent; interior face of male flagellum with or without serrations 31
- 31 Abdominal pleurum II with sclerite extending onto sternum II and occasionally tergum II, sometimes at the expense of sternite or tergite (Fig. 68); mesomeres unfused, may be fused to parameres and apparently absent; pseudostyli absent or, if present, broad or narrow (Figs 68, 71, 72); interior face of male flagellum serrate. [Bovidae] **DAMALINIA (DAMALINIA)**(p. 260)
- Abdominal pleurum II not extending onto sternum II; mesomeres fused, unfused or absent; pseudostyli, if present, not as figured above; interior face of male flagellum lacking serrations 32
- 32 Atria of abdominal spiracles large, clear; mesomer arch fused to b.a.l.s.; parameres broad, asymmetrically deflected (Fig. 64); thorax with setae sparse dorsally in female, but male with median patch of setae on prothorax; head elongate, trapezoid, with deep osculum present (Fig. 63) [Tragulidae] **TRAGULICOLA**(p. 255)
- Atria of abdominal spiracles not large; mesomer arch not fused to b.a.l.s. or, if it is, parameres and mesomeres also fused (Fig. 60); parameres not broad or asymmetrically deflected; thoracic setae less sparse but male thorax lacking central setal patch; head not elongate but rounded, osculum absent or, if present, not deep (Fig. 3) 33
- 33 Parameres fused to mesomeres (Fig. 60); pseudostyli present, apically angular (Fig. 59); gonapophyses broad, truncate (Fig. 58); osculum absent, but anterior margin of head slightly flattened or concave medially, with hyaline border where pulvinus attains margin. [Bovidae] **BISONICOLA**(p. 253)
- Parameres not fused to mesomeres; pseudostyli, if present, apically rounded; gonapophyses

- not broad, and with lobe variably apparent, or, if gonapophyses broad and truncate (*Werneckiella*), then pulvinus not attaining anterior margin of head, which is smoothly rounded and lacks a median hyaline border..... 34
- 34 Gonapophyses broad, truncate; mesomeres of characteristic pentagonal form (Fig. 62). [Equidae and Bovidae]..... **WERNECKIELLA** (p. 255)
- Gonapophyses with more or less discrete lobe (Figs 42, 43); mesomeres, if present, not pentagonal; base of parameres frequently heavily block-like. [Bovidae, Cervidae and Camelidae] (**BOVICOLA** s.l., p. 247) 35
- 35 Species with more or less dense covering of long setae; anterior setae present on abdominal terga, sterna and pleura, slightly shorter than setae of posterior setal rows on these elements (Fig. 47); gonapophyses with very limited lobe formation (Fig. 44) 36
- Species with shorter setae or, if setae long, then sparsely distributed and anterior setae not present on abdominal terga and sterna; gonapophyses generally with more developed lobe (Figs 43, 45) 37
- 36 Sitophore sclerite with posterior arms extended (Fig. 12); male with specialised setae on abdominal tergum II (Fig. 41); mesomeres absent (Fig. 56); female lacks spinose patch on postgenital pleural area **BOVICOLA (SPINIBOVICOLA)** (p. 253)
- Sitophore sclerite with posterior arms not extended; male lacking specialised setae on abdominal tergum II; mesomeres present, fused apically, with median extension (Fig. 57); female with spinose setal patch on postgenital pleural area
BOVICOLA (HOLAKARTIKOS) (p. 251)
- 37 Setae on head long, fine; osculum absent; preantennal sulcus absent; gonapophyses with very distinct lobe of characteristic form (Fig. 43); male genitalia with mesomeres not fused, bipartite (Fig. 55) **BOVICOLA (LEPIKENTRON)** (p. 252)
- Setae on head not long and fine; osculum present or absent; preantennal sulcus present or absent; gonapophyses with less distinct lobe, of different form (Figs 42, 45); male genitalia of different form, mesomeres never bipartite..... **BOVICOLA (BOVICOLA)** (p. 251)

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